THE ECOLOGY OF BAOBABS (*ADANSONIA DIGITATA* L.) IN RELATION TO SUSTAINABLE UTILIZATION IN NORTHERN VENDA, SOUTH AFRICA

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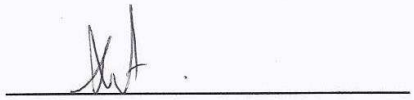
DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any university.



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ABSTRACT

The harvesting and commercialization of non-timber forest products (NTFPs) both present social, economic and environmental challenges. Thousands of NTFPs are harvested from wild populations around the world and the use thereof meets the subsistence and commercial needs of many millions of people. Yet few such products are being sustainably harvested, presenting a threat to the survival of many species. As commercial interest in NTFPs grow, it is increasingly important to understand the biology of the species being harvested. A number of species have oil-bearing seeds which provide ingredients for cosmetic formulations. Baobab ((*Adansonia digitata* L.) seed oil, is one such ingredient, which has rapidly become popular on global markets.

Baobabs are an iconic, very long-lived, African savanna tree species known throughout their range as a source of food, fibre and medicine, yet global demand for its fruit derivatives (both seed oil and fruit pulp) have raised concerns about sustainability. This study undertook to investigate the ecological aspects of fruit harvesting and to document the socio-economic benefits of commercializing the fruit.

Research was conducted in northern Venda, Limpopo Province, South Africa. Population dynamics, fruit production, phenology and recruitment were investigated in five land-use types, namely: nature reserves, rocky outcrops and plains, representing natural land-use types, and fields and villages representing human-modified land-use types. Density of trees was determined from transects, fruit and flower counts were done on 106 trees over 2-3 seasons, seed viability and seedling/sapling survival rates were determined and interviews with harvesters were conducted in villages across the study area. Data analysis used standard univariate statistical methods and the results were used to create a stage structured population projection matrix model.

Villages and fields had higher densities of trees (2.16±0.44 and 1.13±0.52 plants/ha) than plains and rocky outcrops (0.96±0.25 and 0.83±0.24 plants/ha). All land-use types had positively skewed size-class distribution (SCD) curves and negative to flat SCD slopes indicating low recruitment. Quotients and the permutation index suggest that recruitment and mortality are episodic events, but nonetheless that the population has been stable. Mature fruit production was higher in villages and fields (89.59±34.61; 88.26±32.20fruit/tree) than nature reserves, plains and rocky-outcrops (1.90±1.15; 28.64±12.56; 12.56±5.59 fruit/tree). Predation on immature fruit by baboons resulted in 58-85% loss. Inter-annual variation in fruit production was significant, with a 2½-fold difference between the highest and lowest years. Flowering followed a steady-state pattern, lasting 1-5 months and peaking in November. Mean flower numbers/tree (711±72 and 287±33) varied significantly between sequential years, but not fruit-set (average of 20±4%). Baobab seed exhibited high viability (>91%) and formed persistent seed banks. Seed production was substantial (5500±2334

seed/ha); thus recruitment does not appear to be seed-limited except in areas where baboons are found. Seedling emergence was staggered over two growing seasons. In plots where livestock were excluded (closed plots) 6.33% of seed emerged with a mean natural germination rate of 328±28 days and of these 94.44% died of moisture stress and insect browsing within 21±5 days. In open plots only 2% of the seeds emerged with a germination rate of 377±5 days and all of them died from livestock browsing within 12±5 days. Planted sapling survival in closed plots (65%) was significantly better than in open plots (10%) where repeated livestock browsing and trampling was responsible for high mortality rates. Matrix model output indicated that high livestock numbers and baboon predation of fruit cause population decline. Under zero to moderate livestock numbers, populations in communal land-use types are able to tolerate fruit harvest rates of between 33-90%.

Harvesters were marginalized people to whom the sale of baobab fruit had an income value 4 times higher than its subsistence value. The sale of baobab fruit contributed 38% to the overall cash income received from NTFP sales, helping to alleviate poverty and increase access to a cash economy.

It was concluded that the management of baobab populations require an integrated approach incorporating human needs and environmental variables. The long-lived nature of baobab trees provides a buffer against short-term pressures (an excellent example of the ‘storage effect’), but unabated environmental degradation and climate change threaten populations. It is recommended that government agencies, businesses, traditional authorities and harvesters invest in strategies that will protect baobabs and boost recruitment to safeguard future populations and ensure multi-generational benefits for rural people.

DEDICATION

I dedicate this thesis to my husband, Casper Venter and
to the memory of my mother, Penny Bristow.

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GLOSSARY OF FREQUENTLY USED TERMS

Adult plant: A plant that has reached reproductive size or age.

Browsers: An animal that utilises the portion of the woody vegetation that is available for consumption by animals (Tainton, 1999).

Carrying capacity: Potential of an area to support livestock through grazing and/or browsing over an extended number of years without deterioration to the overall ecosystem (Tainton, 1999).

Cash-value: The monetary or sale value of products.

Commercial harvesting: The collection and sale of plant products intended for outside markets, such as national or international markets. This usually means that higher volumes are harvested and with a higher frequency and intensity.

Degradation: Loss of economic potential to produce goods/services of direct human-use value; loss of ecological function necessary to maintain ecosystem processes; loss of biodiversity at ecosystem, community or genetic level.

Density: Number of plants (or animals) per unit area.

Diameter Breast Height (DBH): The diameter of a tree 1.3 meters above the ground.

Direct-use: See subsistence use.

Emergence: The appearance of a seedling shoot at the soil surface after germination (Fenner and Thompson, 2005).

Fields: Areas cleared of herbaceous and woody vegetation for planting crops. In the context of this study, fields are not irrigated and are often left fallow. Some indigenous fruit bearing trees , such as adult and sub-adult baobabs, are not cleared. Fields are often situated close to villages.

Fruit production: The total number of fruit produced by an individual tree or a group of trees in one season.

Fruit-set: Number of flowers that become fruit on an individual tree. This is calculated by dividing the number of fruit produced by the number of flowers produced per tree, per season and expressing it as a percentage.

Juvenile: See Sub-adult.

Land-use types: Areas of land that are used for different purposes and thus have certain types of impacts on the natural vegetation and ecosystem. Land-use types used in this study were villages, fields, plains, rocky out-crops and nature reserves.

Livelihood: The complex and diverse ways in which marginalised people provide for themselves and their families. These frequently comprise a range of different activities which depend on access to a variety of capital assets including non-timber forest products (Clarke and Grundy, 2004).

Livestock: Domestic animals used for production purposes and in the context of this study are mostly goats and cows.

Marginalized people: People who are unable to substantially improve their livelihoods because of a lack of education, poverty, social status or gender.

Microsite: The immediate environment within which a seedling is growing.

Nature Reserves: These are areas under the control of provincial authorities and the main management objective is the conservation of local plant and animal species. Collection of non-timber forest products is generally not allowed in these areas.

Non-timber forest product (NTFP): A wild biological resource that is harvested by rural households for domestic consumption or trade with no or limited capital investment. This includes the collection of firewood and poles, but excludes timber felling (Shackleton *et al.*, 2007).

Phenology: The timing or seasonality of specific biological events (for example, leaf fall, growth, or the production of flowers and fruit) (Peters, 1996).

Plains: Open access areas outside of villages and fields where livestock are allowed to graze and where non-timber forest products can be collected. Also be referred to as 'rangelands'.

Population: A group of organisms, all of the same species, that occupies a particular area (Peters, 1996).

Population dynamics: The change in the size and structure of a population over time (Peters, 1996).

Poverty alleviation: The lasting improvement in the livelihood asset base even if households are still below the poverty line.

Rangeland: Indigenous vegetation used for grazing and/or browsing which may be composed of any of a number of plant growth forms (Veld) (Tainton, 1999).

Recruitment: The addition of new individuals into a population through seedling establishment (Peters, 1996).

Regeneration: Population recruitment arising from seeds and seedling establishment or vegetative growth (Peters, 1996).

Rocky outcrops: In the context of this study, these are areas in plains that are dominated by rock extrusions inhabited by baboon populations and where livestock do not often graze/browse.

Sapling: Defined here as a young plant, 1-3 years old, which has a swollen tap root (storage organ) allowing it to survive through winter and to recover from browsing.

Savanna: Vegetation with a grass dominated herbaceous layer and scattered low to tall trees (Mucina and Rutherford, 2006).

Seedling: Defined here as newly germinated plant, 0-1 year old, which has not yet developed a swollen tap root (storage organ) necessary for survival through winter.

Size-class distribution (SCD): A graphical representation of a population structure. In this case a number of plants represented by stem diameter size categories of equivalent intervals.

Storage effect: During years with conditions favourable for seedling regeneration, a species can establish a cohort of juveniles and once established these individuals are able to persist in adverse conditions. Reproductive potential is thus "stored" between generations, allowing the population to recruit strongly when conditions are favourable (Chesson and Warner, 1981)

Sub-adult: Defined here as a young plant which has lost its swollen tap root, but that has not yet reached reproductive size, usually < 100cm dbh (diameter breast height).

Subsistence use: The use of plant/animal products for household needs, not sold for cash income.

Sustainable harvesting: Harvesting that allows for a non-declining, continual supply of the product being utilized; harvesting that has negligible impact on the structure and dynamics of the plant population being exploited (Peters, 1996).

Trampling: The damage to leaves and stems of young plants caused by the hooves of livestock (usually cattle).

Villages: A land-use type consisting of concentrations of human dwellings and livestock paddocks and home-gardens. In the study area, most villages have electricity, communal taps and are interspersed with spaza shops (locally owned shops). There is usually a high human impact on the natural vegetation in and around villages.

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Chapter 1

Introduction

1. General Introduction and Review

1.1 Context

Forests and woodlands across the world provide plant products that support the livelihoods of millions of people (Shackleton and Gumbo, 2010). In particular, many poor and marginalized people who live in the savanna woodlands in Africa rely on plant products for their survival. Plant products, or Non-Timber Forest Products (NTFPs), are important for food, nutrition, shelter and energy and, in addition to subsistence use, are often sold to generate a cash income (Dovie *et al.*, 2002; Shackleton and Shackleton, 2004). The immense importance of these plant resources has meant that studies are increasingly focused on their sustainable harvest and management. For example studies have looked at the impact on the growth and survival of trees from the harvesting of bark, leaves and wood and the effects on regeneration of harvesting flowers and fruit (Witkowski *et al.*, 1994; Bernal, 1998; Botha *et al.*, 2002, 2004; Geldenhuys, 2004; Luoga *et al.*, 2004; McKean, 2004).

A number of wild species have oil-bearing seeds which have become popular ingredients in cosmetic formulations. Species that are wild-harvested for their seed oil include *Sclerocarya birrea* (marula), *Kigelia Africana (African Sausage Tree), Trichilia emetica (Mafura)* and *Adansonia digitata* (baobab). Where these species are found in rural areas, commercialization is seen as an opportunity to uplift the poor and marginalized people who live there (Welford and Le Breton, 2008). As cosmetic oils have become more popular around the world, it is predicted that demand will grow (Gruenwald and Galizia, 2005). Thus understanding the impact that harvesting will have on wild populations has become very important, and not all species have been adequately studied. In South Africa, the two most popular indigenous tree species used for seed oil production are marula and baobab. The importance of marula fruit as a food item has meant that substantial research has already been done on the ecology and utilization of that tree (Shackleton, 2002; Ham, 2004; Emanuel *et al.*, 2005; Helm *et al.*, 2011). However, for baobab, little was known about the impact of harvesting its fruit.

Baobabs (*Adansonia digitata* L., family Malvaceae, subfamily Bombacoideae, also known as kremetartboom in Afrikaans or Muvhuyu in TshiVenda), not only provide seed oil but are also used for food, fibre and medicine. Fruit and leaves are an important source of nutrition and bark is used for fiber. Baobab products have been bartered and sold in urban and informal markets across Africa for many hundreds of years (Sidibe and Williams, 2002). The more recent interest in baobab seed oil has resulted in a surge of fruit harvesting operations in many parts of the tree's distribution.

The commercial harvesting of baobab fruit began in the Venda area of Limpopo Province, South Africa (Fig. 1) in 2005. Fruit were collected from the surrounding communal lands, fields and villages by harvesters living in the area, mainly unemployed women. The harvesters cracked the fruit to remove the seed and fruit pulp and sold these to a locally-based company. The company used the seeds to make oil and packaged the fruit pulp. These fruit derivatives were then sold to the local and international cosmetic and ingredient markets. The collection of large quantities of fruit to meet these new demands prompted questions about the sustainability of harvesting. This study was thus initiated in 2006 to investigate the impact of harvesting on the tree population and to recommend sustainable harvesting levels.

In order to assess the sustainability of fruit harvesting, a thorough understanding of the biology and ecology of the local baobab population was required. In addition to this, understanding the socio-economic impact of commercializing this resource is essential. Thus the study focused on the following: 1) baobab tree population dynamics; 2) fruit productivity; 3) phenology; 4) recruitment; 5) socio-economics and 6) setting sustainable fruit harvest levels.

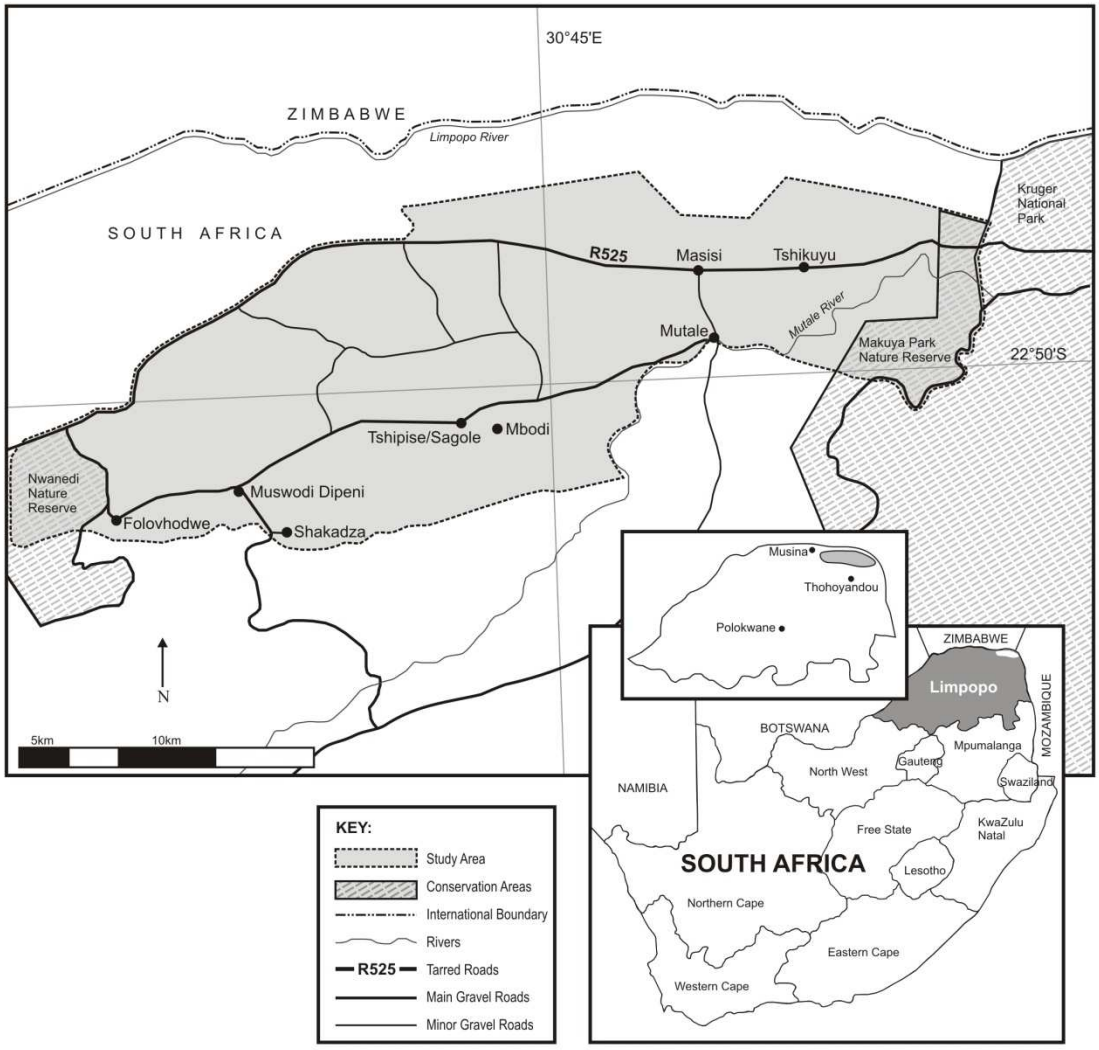

Figure 1. Location of study area in Limpopo Province, South Africa.

1.2 Population dynamics

The study of plant population dynamics involves assessing changes in a population with regard to its size, density and age distribution (Miller, 1998). Plant population ecology deals with the factors that affect current, past and future trends within and between populations (Silverton, 1997). Many ecological studies have used techniques of predicting population trends from size-class distributions (SCDs) (Condit *et al.*, 1998). Large numbers of juvenile relative to adult trees typically form an inverse J-shaped SCD, which is usually taken to mean that the population is healthy. Bell-shaped SCDs, where there are fewer juvenile than adult trees, represents a population in decline. However, bell-shaped SCDs

are not necessarily a problem for larger, longer-lived species, where trees can sustain population levels with low or episodic recruitment (Condit *et al.*, 1998).

Population surveys are often done on baobabs, probably because they are noticeable in the landscape and easy to count. Most such studies have found that baobabs exhibit either positively skewed or bell-shaped SCDs, with many trees falling in the middle (100-300 cm dbh) size class (Hofmeyr, 2003; Dhillion and Gustad, 2004; Assogbadjo *et al.*, 2005; Chirwa *et al.*, 2006; Edkins *et al.*, 2007). Densities of baobabs have been found to vary between landscapes. In West African countries baobabs appear to have higher densities of juveniles in villages and fields than in fallows (Dhillion and Gustad, 2004; Assogbadjo *et al.*, 2005; Duvall, 2007), whereas the opposite is found in southern African countries where juveniles are lacking in villages and fields and are more plentiful in natural areas (Chirwa *et al.*, 2006). In nature reserves, young baobabs are often confined to hillsides and rocky outcrops where they escape elephant damage (Hofmeyr, 2003; Edkins *et al.*, 2007). In all studies, the lack of seedlings is mentioned as a concern, but it is generally felt that, due to the long-lived nature of baobabs, populations are buffered by a 'storage effect' allowing them to persist through highly episodic recruitment events. However, circumstances are changing with higher demands on the resource (Buchmann *et al.*, 2010), increased land transformation (Coetzer *et al.*, 2010) and threats of climate change (Cuni Sanchez *et al.*, 2011b). Thus the past population dynamics may not be an adequate predictor of future trends. A study of the current standing stock of trees in Venda may help us determine if past trends have resulted in a stable population. Analysis and comparisons of the size-class distributions and densities of trees in different land-use types will provide insights into how the population is currently structured. Hopefully, this will help to guide the management of the baobab population in this area.

1.3 Fruit productivity

Perennial plants start to produce fruit once they have reached a certain size or age, and the size of the crop can be strongly influenced by environmental conditions. Once a plant reaches the reproductive stage of its life, its capacity to produce fruit usually increases as it gets larger and is influenced by the amount of resources the plant allocates to reproduction versus growth and survival (Fenner and Thompson, 2005). Resource factors external to the plant, such as site and climate, also influence the ability of plants to reproduce (Tilman, 1997). Plants need light, water and inorganic nutrients to grow and survive; thus large fruit/seed crop sizes are common when resources are plentiful, but smaller when resources are limited (Goldwin, 1992; Fenner and Thompson, 2005). These resources vary between growing sites and between seasons; thus competition for and limitation of these resources has an influence on fecundity (Fenner and Thompson, 2005).

Inter-annual variation, seasonality and fruit predation are the principal factors that commonly influence fruit production. A large crop of fruit in one year can result in a lowering of available resources and result in a small crop the following year (Fenner and Thompson, 2005). The size and quantity of fruit produced can also be attributed to timing. Fruit produced earlier in the season has longer access to available nutrients and water than fruit produced later in the season. Also larger fruit constitute sinks that can divert nutrients away from late-developing fruit (Fenner and Thompson, 2005).

Baobab fruit and seed production has also been shown to be affected by environmental and genetic factors. Assogbadjo *et al.* (2005) studied the productivity of baobab trees across three climatic zones in Benin, and found that there were significant differences in the sizes of the trees, number of fruit produced and the pulp, seed and kernel productivity between these climatic zones. Similarly, fruit collected from Burkina Faso, Mali and Niger were found to vary in weight along precipitation gradients (Parkouda *et al.*, 2011). Baobab leaves are an important food in West Africa and are harvested in large quantities, and it has been shown that removing leaves significantly reduces fruit production. It is presumed that the removal of the leaves damages growing tips and reduces the ability of trees to photosynthesize, thus reducing fruit production (Schumann *et al.*, 2010). Developing fruit are a rich source of food, and are eaten and parasitized by a variety of animals including insects, birds and mammals (Hulme, 2001). Baboons (*Papio ursinus* and *P. anubis*) are known to feed on immature baobab fruit early in the wet season, when there are few other fruit available, and this is thought to have a negative effect on seed production (Lieberman *et al.*, 1979; Pochron, 2005; Kunz and Linsenmair, 2007). De Smedt *et al.* (2011), also working in West Africa, measured variation in shell, pulp and seed weight and found significant differences between provenances and between trees of the same provenance, suggesting genetic control of certain fruit traits. Thus it is clear that, in order to manage fruit-harvesting operations in each population being harvested, information on baobab fruit production and how this varies between trees, land-use types and between years should be understood.

1.3 Phenology

Phenology is the study of periodic biological events and the description of seasonal growth, development and reproduction (Begon *et al.*, 1990). In trees, the annual timing of leaf flush and flowering will usually be governed by environmental cues, such as light intensity, photoperiod, temperature and water availability (Lyndon, 1992). It is important to have an in-depth understanding of baobab phenology, as this has a significant impact on population functioning and fruit production.

Baobabs flush leaves and produce flowers during the wet season and are leafless during the dry season (Wickens, 1982). Before the onset of rain, stem water supports the first flush of leaves (Chapotin *et al.*, 2006). The timing of leaf flush and flowering varies greatly between localities with longer seasons on the equator, and shorter seasons at higher latitudes. Wickens (1982) observed that flowering in the Sudan occurred throughout the year except at the height of the dry season, whereas in southern and east Africa, flowering starts to occurs just before the onset of the rainy season and usually lasts only five months (Swanepoel, 1993; Assogbadjo *et al.*, 2005). During the flowering season, trees produce 10-50 flowers per night, each flower lasting only 24 hours (Von Breitenbach and Von Breitenbach, 1974). Fruit develops 4-6 months after flowering and most fruit mature during the peak of the dry season (Sidibe and Williams, 2002; Assogbadjo *et al.*, 2005). In southern Africa, baobab fruit start ripening between April and May and mature in June/July (Palgrave, 1983) and in the northern hemisphere (Benin), fruit mature in December and January (Assogbadjo *et al.*, 2005).

The relative success of flowers to produce fruit is called 'fruit set' (Goldwin, 1992). Often there is a long period between flowering and fruit ripening, during which time environmental and biological conditions can have a major impact on the success of fruit set (Goldwin, 1992; Fenner and Thompson, 2005). Very little has been known about baobab fruit set. As mentioned above, leaf harvesting is known to reduce fruit production, possibly due to reduced photosynthesis (Dhillion and Gustad, 2004; Schumann *et al.*, 2010). Elephants cause severe damage to baobabs when they strip bark off trees, which could also lead to reduced flowering and fruiting (Swanepoel, 1993). Pollination failure is common in plants, particularly in species that are animal-pollinated (Howe and Westley, 1997; Fenner and Thompson, 2005). Bats are presumed to be the main pollinators of baobabs (Baum, 1995a). However, although baobab flower morphology is best suited to bat pollination (Baker, 1961), moths and hymenopterous insects also visit baobab flowers (Watson, 2007; Wickens and Lowe, 2008), which may lead to reduced fecundity due to self-pollination, it being presumed that *A. digitata* is self-incompatible (Baum, 1995a). Low fruit-set may thus reflect a form of sexual dimorphism, and the belief in the existence of male and female baobab trees is common throughout Africa (Assogbadjo *et al.*, 2008)(Colin Bristow and Diana Mayne, personal communications). Nothing is known about the phenology of baobab trees in Venda, and if similar trends are found in that region. A thorough understanding of the phenology of this population would be required in order to make informed management recommendations on this basis.

1.4 Recruitment

Baobab seedlings and saplings are absent from many populations in southern Africa, suggesting that there are significant recruitment bottlenecks (Hofmeyr, 2003; Chirwa *et al.*, 2006). Recruitment could be seed-limited (not enough viable seed being available) or microsite limited, where seedlings do not survive because of environmental factors. Germination of baobab seeds in the wild is known to be very poor (De Villiers, 1951), yet, under nursery conditions, germination percentages are usually 20-50% and, when pre-treated with concentrated sulphuric acid, exhibit germination percentages of up to 90% (Danthu *et al.*, 1995; Razanameharizaka *et al.*, 2006; Assogbadjo *et al.*, 2010). Recent work has shown that the substrate used for germination and the climatic zone from which seeds are collected both have a significant influence on both germination and seedling growth (Assogbadjo *et al.*, 2010; Cuni Sanchez *et al.*, 2011a). Within the first two years of growth, baobabs produce an underground tuber or tap root (Cuni Sanchez *et al.*, 2011a), suggesting that resprouting of young plants is an important life-history strategy. However domestic animals (cattle, sheep and goats) are blamed for causing poor recruitment in many parts of Africa (Sidibe and Williams, 2002; Dhillion and Gustad, 2004; Assogbadjo *et al.*, 2005; Chirwa *et al.*, 2006). Identifying and quantifying recruitment bottlenecks therefore provides important information for assessing future population trends. It also helps quantify the effect of fruit harvesting on recruitment so as to aid sustainable harvesting.

1.5 Soco-economics

Throughout their distribution, baobabs are used for food, medicine and fibre (Owen, 1970). Baobab fruit pulp is rich in Vitamin C and calcium (Osman, 2004). As a food, it is used to supplement the diets of children, elderly people and people suffering from diarrhoea and malnutrition. Baobab leaves are rich in essential amino acids and minerals such as tryptophan, niacin, calcium, iron, potassium and magnesium (Yazzie *et al.*, 1994). The bark has medicinal properties and is used to treat fevers. Rope, baskets and nets are made from baobab bark fibres (Sidibe and Williams, 2002).

The collection and trade of baobab products is seasonal, reaching their peak in the dry season when other products are scarce (Sidibe and Williams, 2002). The recent commercialization of processed baobab products such as baobab seed oil and baobab fruit pulp has lead to even greater cash returns for harvesters (Gruenwald and Galizia, 2005). However, concerns have been raised regarding the impact that commercialization will have on subsistence users, particularly in West Africa (Buchmann *et al.*, 2010). In southern Africa, by contrast, baobab fruit are regarded as relatively underutilized and that

commercializing this resource will make a significant contribution to alleviating poverty in rural areas (Gruenwald and Galizia, 2005).

There is thus a need to determine the subsistence and cash value of baobab fruit and to describe the socio-economic impact commercialization of this resource will have on rural people in southern Africa. Based on what may be found, recommendations can be made regarding the sustainable and equitable distribution of the resource.

1.6 Sustainable harvest levels

The sustainable utilization of Non-Timber Forest Products (NTFP) is essential for the conservation of the plants and for the livelihoods of rural people who depend on these resources (Ticktin, 2004). However, many studies have found that the utilization of NTFPs is often unsustainable, especially when harvesting affects the survival of the plant (Boot and Gullison, 1994; Carter, 1996; Shackleton, 1996; Ticktin, 2004). Fortunately, the harvesting of fruit and seed has the least impact on population structure, with high degrees of tolerance to harvesting found (Ticktin, 2004). High tolerance levels can be attributed to three factors: firstly, the parent trees not being removed or damaged; secondly, the occurrence of continuous rejuvenation and thirdly, trees having long reproductive periods (Bernal, 1998; Zuidema and Boot, 2002).

Stage-based population matrix models can be used to assess the impacts of different harvesting regimes on population structure and viability. By integrating life-stage data and different harvesting intensities, models can predict how the populations would respond (Bernal, 1998; Zuidema and Boot, 2002; Emanuel *et al.*, 2005). Matrix models are useful because of their standardized form, relatively low data requirements and also because they can be used as tools to examine demographic disturbances (Desmet *et al.*, 1996). Matrix models applied to other species, e.g. Brazil nut (*Bertholletia excelsa*), vegetable ivory palm (*Phytelephas seemannii*) and Marula (*Sclerocarya birrea*), found that there was high tolerance to seed removal because of the long-lived nature of the trees.

Despite the high use of baobab products throughout Africa and the growing world demand for fruit derivatives, there appears to have been no previous attempt to establish sustainable yield sizes for this tree. So, drawing on the ecological knowledge gained in this study ─ for example information on population size, fruit production, phenology and recruitment ─ a population matrix model was constructed to guide sustainable harvests and make management recommendations that would mitigate negative effects on the population.

2. Research Rationale and Objectives

Baobab fruits have been harvested throughout Africa for many thousands of years (Wickens and Lowe, 2008). The fruit is a source of food and is also bartered and sold to generate a cash income that supports the livelihoods of many rural people (Sidibe and Williams, 2002). However, over the last decade the demand for baobab fruit has moved into the global market where derivatives of the fruit, namely seed oil and fruit pulp, are growing in popularity (Gruenwald and Galizia, 2005). This has led to concerns about the effect that fruit harvesting would have on baobab populations, yet not enough was known about baobab ecology to guide sustainable harvest levels. The aim of this study was to investigate the population dynamics, phenology, fruit production and recruitment of baobab populations in communal land-use types. This information would be used to construct a population matrix model to determine sustainable fruit harvesting levels. The importance of the tree in one of the poorest areas in South Africa, and how the utilization of the fruit could contribute to local peoples' livelihoods, would be explored and assessed. The synthesis and integration of all aspects of this study should represent a considerable advancement in our understanding of the ecology of long-lived trees.

The objectives of the study were:

1) To determine the population size, density and size-class distribution of baobab trees in different land-use, vegetation and soil types.
2) To estimate fruit production and how it would vary between size classes, land-use types and successive years.
3) To describe the phenology of the baobab population at the southern limit of its distribution.
4) To assess recruitment in terms of seed production and seedling/sapling survival.
5) To document the socio-economic trends resulting from the commercializing of baobab fruit in northern Venda.
6) To establish sustainable harvest levels and recommend methods and management interventions for the collection of baobab fruit.

3. Thesis Structure

The chapters of this thesis, with the exception of the Introduction and Synthesis, are autonomous and have been written in the format of scientific papers. Chapters 2 and 4 are papers published in *Forest Ecology and Management*; Chapter 3 is a paper given at the Natural Forests and Woodlands Symposium, held in Richards Bay, South Africa in April

2011; Chapters 5, 6 and 7 are submitted papers which are currently under review for internationally recognised journals, and Chapter 8 will be submitted when the previous three chapters are accepted for publication (Fig 2). In the circumstances it is unavoidable that there should be some repetition between chapters, for example in the descriptions of the study region and the study species.

Brief Chapter outlines

Chapter 1 is an introduction and establishes the rationale and objectives of the thesis.

Chapter 2 describes baobab population structure and trends in four communal land-use types (plains, rocky outcrops, fields and villages). This was done by analysing tree densities and size-class distributions and then using these to generate permutation indexes and quotients to indicate population stability (Fig. 3A). This chapter thus addresses Objective 1 (Fig. 2).

Chapter 3 describes baobab population trends between different vegetation and soil types and between human-modified and natural landscapes. This was done by analysing tree densities, size-class distributions and life-stage densities (Fig. 3A). This chapter thus addresses further aspects of Objective 1 (Fig. 2).

Chapter 4 examines baobab fruit yields by combining demographic and fruit production data. Fruit production information was collected across five land-use types and over three years. This allowed the assessment of differences in fruit production between tree sizes, land-use types and successive years (Fig. 3B). This chapter addresses Objective 2 (Fig. 2).

Chapter 5 describes the phenology of baobabs at the southern limit of their distribution. It gives quantitative data on the timing and duration of leaf flush. It also gives information on flowering and fruit-set and the differences in these between life-stages, tree sizes and land-use types. The chapter discusses the mechanisms that underlie flowering and fruit-set patterns and the belief that there are male and female trees (Fig 3C). This chapter thus addresses Objective 3 (Fig. 2).

Chapter 6 determines whether baobab recruitment is seed-limited or micro-site limited. Seed production, viability and persistence were studied to evaluate seed limitation. Micro-site limitation was investigated by evaluating seedling emergence under natural conditions, and measuring the effect of seasonal variation in rainfall the presence of livestock on seedling and sapling survival (Fig 3D). This chapter thus addresses Objective 4 (Fig. 2).

Chapter 7 focuses on the socio-economic value of baobab fruit. This chapter determines the subsistence and income value of baobab fruit and describes the positive and negative

effects of commercialization. It also describes the socio-economic background of the harvesters involved in collecting baobab fruit, and their perception of the ecology and management of the resource. Based on these findings, the implications of commercialising baobab fruit are discussed and recommendations are made regarding sustainable and equitable commercialization (Fig 2E). This chapter thus addresses Objective 5 (Fig. 2).

Chapter 8 draws on the ecological knowledge gained from the work described in previous chapters to determine population trends under different levels of livestock numbers and fruit harvesting. This is done by building a deterministic stage-based population projection matrix model and using variables on fruit yield, germination/emergence rate, survival rates for each life stage, and number of years an individual would spend in each life stage. This chapter thus addresses Objective 6 (Fig. 2).

Chapter 9 synthesizes the overall findings of this research project, highlights the unique aspects of the study, and identifies areas for further research and makes management recommendations.

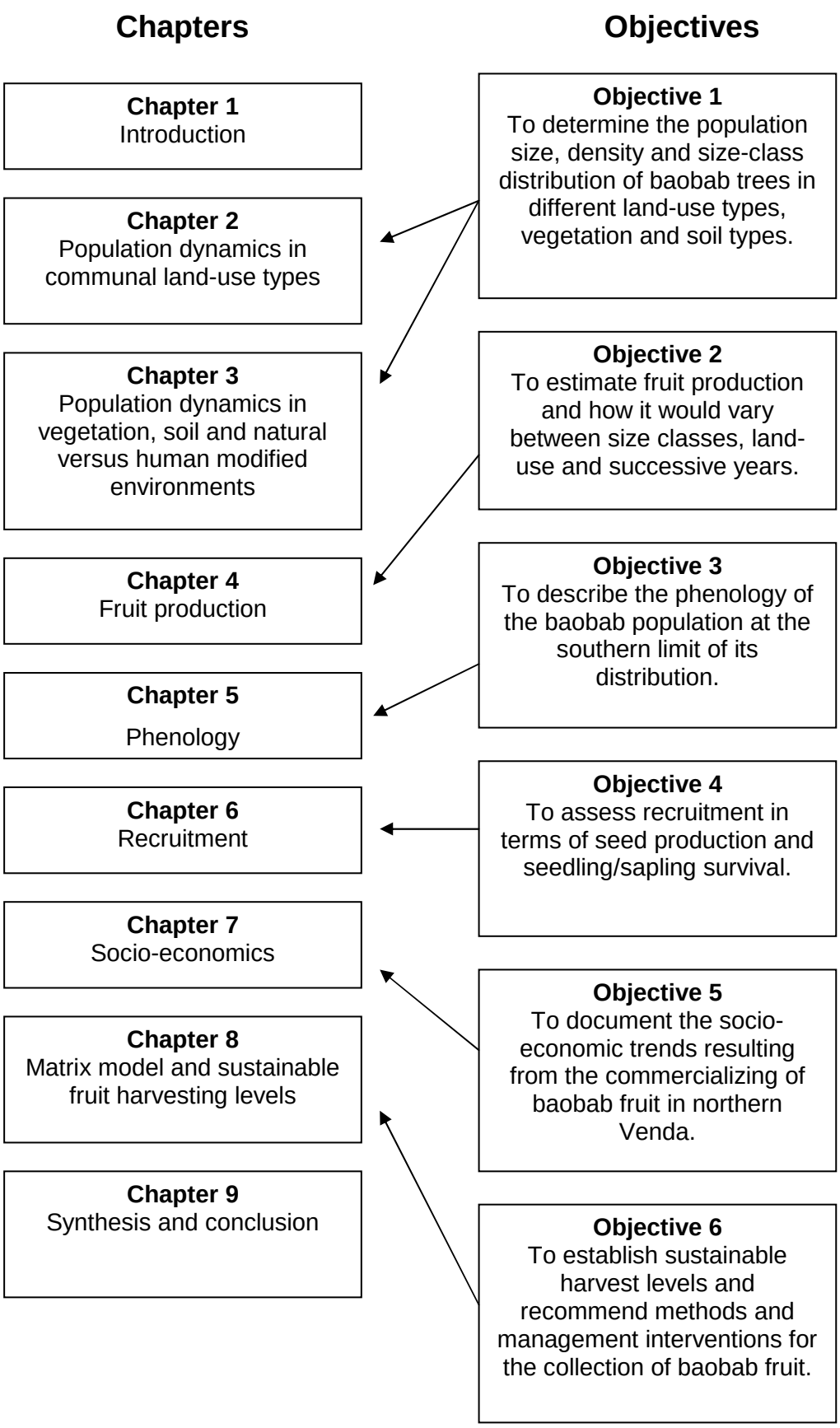

Figure 2. The overall PhD thesis structure, indicating the relationship between the chapters and the objectives.

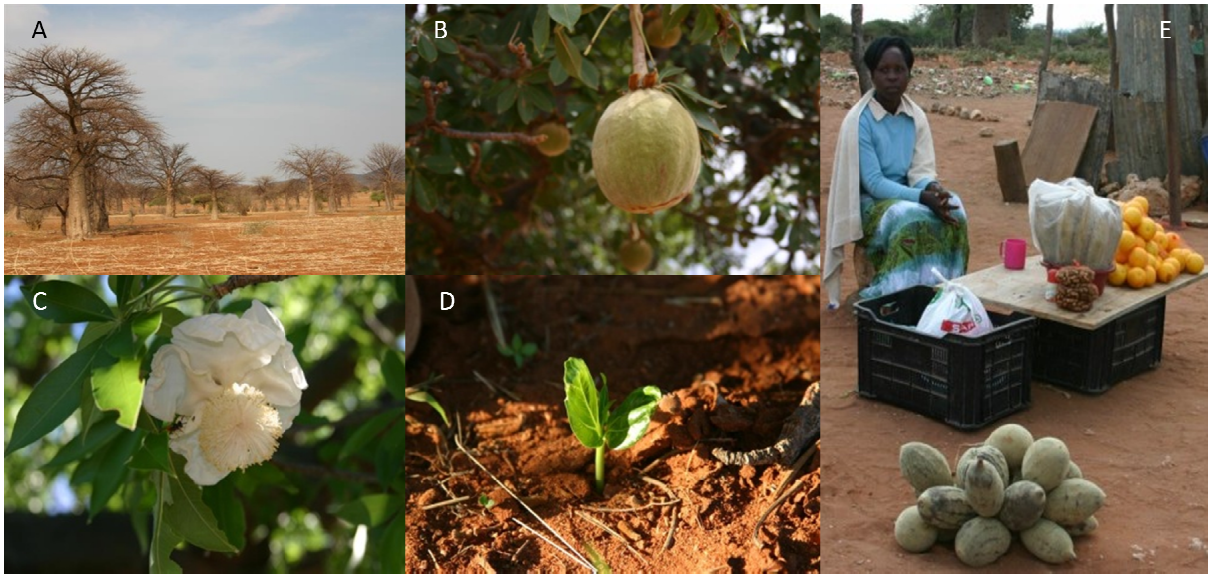

Figure 3. Photographs illustrating baobab population structure (A), fruit production (B), flowering (C), seedling emergence (D) and woman selling baobab fruit for cash income (E).

4. Study Region

The study area of approximately 1000 km^2 is confined to the northernmost part of Venda, centering on 30º45' E and 22º50' S. Venda falls in the Mutale Municipal Area in the northernmost section of Limpopo Province, South Africa. The study area is bordered by the Limpopo River to the north, the Kruger National Park to the east , the northern slopes of the Soutpansberg Mountains to the south, and the western boundary of Nwanedi Nature Reserve to the west (Fig. 1).

It is a semi-arid summer rainfall area, characterized by hot summers (October-March) and mild winters (April-September). The mean annual summer rainfall falls between 334mm in the west and 423mm in the east (Mucina and Rutherford, 2006). The average daily minimum temperature is 16.8°C with an average daily maximum of 31.3°C. The lowest temperatures occur in June with an average minimum of 7.9°C, and the highest during November with an average maximum of 34.7°C. Frost seldom occurs (Mucina and Rutherford, 2006).

Where vegetation is concerned, the area falls within the Savanna Biome and is divided into Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makuleke Sandy Bushveld by Mucina & Rutherford (2006). This bioregion unit is dominated by *Colophospermum mopane, Terminalia sericea, Grewia flava* and *Combretum apiculatum*. Butt *et al*. (1994) describe this region as low sparse woodland, with an average tree height of 4-5 m and tree cover of 20%.

There are a number of birds and mammal species are associated with baobabs in the region. Mosque swallow (*Hirundo senegalensis*), Grey-headed Parrot (*Poicephalus fuscicollis suahelicus*) (Symes and Perrin, 2004) and Barn Owl (*Tyto alba*) use hollows to breed *(pers. obs.*). Most notable for the region, is the largest known colony of (over 300) Mottled spinetails (*Telecanthura ussheri*) in a hollow baobab. Red-billed Buffalo Weaver (*Bubalornis niger*) and Red-headed Weaver (*Anaplectes rubriceps*) nests are common within the tree canopies (pers. obs.). Mammal associations include Chacma Baboon (*Papio cynocephalus ursinus*), Vervet Monkey (*Cercopithecus aehtiops)* and Small-spotted Genet (*Genetta genetta*) (*pers. obs*.).

The area lies at an altitude of around 400 m above sea level. The topography is gently undulating with a narrow sandstone ridge running east-west through the center of the study area. A combination of Karoo sandstone sediments and basalt underlies most of the area.

Management and ownership of the land and its resources is determined by local customs and structures. People have lived in this area for many thousands of years. Archaeological records show that this area has been inhabited, on and off since the Early Stone Age (Deacon and Deacon, 1991). Numerous rock art sites across the study area are evidence of Late Stone Age occupation (Eastwood and Eastwood, 2006). Iron Age and recent occupation periods include those designated as Mapungubwe, Eiland, Khami, Moloko and Letaba (Venda) (Loubser, 1991; Huffman, 2007). The people who currently live in the area belong to the BaVenda ethnic group. The 2001 population census estimated 108 215 people living in this area, with a density of approximately 200 people per square km (Statistics-South-Africa, 2001).

For the purposes of this study, the chosen area has been divided into four broad land-use types: villages, fields, rangelands and rocky out-crops. To the west and east of the study area are two provincial nature reserves, namely Nwanedi Nature Reserve and Makuya Park Nature Reserve. Villages are structured on grid-based 1 ha plots, each plot having a dwelling, either a mud rondavel or brick structure. Most plots include a vegetable garden and trees. Common trees found in the villages are baobab (*Adansonia digitata*), marula (*Sclerocarya birrea*) and shepherd's tree (*Boscia albitrunca*). Water is accessed by boreholes with communally-shared water points scattered throughout the villages. Fields are used in the wet season for dryland cropping. Millet and sorghum are the most commonly planted crops. These are sometimes intermixed with groundnuts, pumpkins and watermelons. As fields are not irrigated, fertilizers and pesticides are seldom used. Rangelands are those communal areas outside villages which are used for livestock grazing and for the collection of non-timber forest products. Rocky outcrops form part of the rangelands, but have been separated because of topographic differences.

5. Study Species

Adansonia digitata L. is one of eight species of baobabs in the genus *Adansonia* (Malvaceae subfamily Bombacoideae). Six species occur in Madagascar, one in Australia and one, *A. digitata*, in mainland Africa (Baum, 1995b). African baobabs are widely distributed and are found in west, east and southern Africa (Fig. 4). In South Africa the population is limited to the Limpopo River valley, north of the Soutpansberg Mountains, with only some isolated trees occurring further south.

In Africa baobabs are found mostly in the drier plant communities of the Sudano-Zambesian lowlands where annual rainfall is 200-800 mm annually (Wickens, 1982). In southern Africa they are associated with *Colophospermum* (mopane)*, Cordyla* and *Kigelia* woodlands in low-lying, dry, hot and frost-free areas. They occur on a variety of soil types, but seem to do best on deep, well-drained soils (Wickens, 1982).

Baobabs are characterized by swollen trunks and palmately compound leaves. The trunks consist of soft, fibrous wood that can store water. The leaves of juvenile trees are simple and gradually change to 5-7 foliate compound leaves as the tree gets older. Flowers are borne in the axils of leaves and comprise a single, large, odoriferous white flower made up of both male and female reproductive parts. The fruits are large, ovoid, and covered in a yellow/green velvety indumentum. The pericarp is woody and indehiscent. Seeds are reniform, embedded in a soft dry matrix (Baum, 1995b).

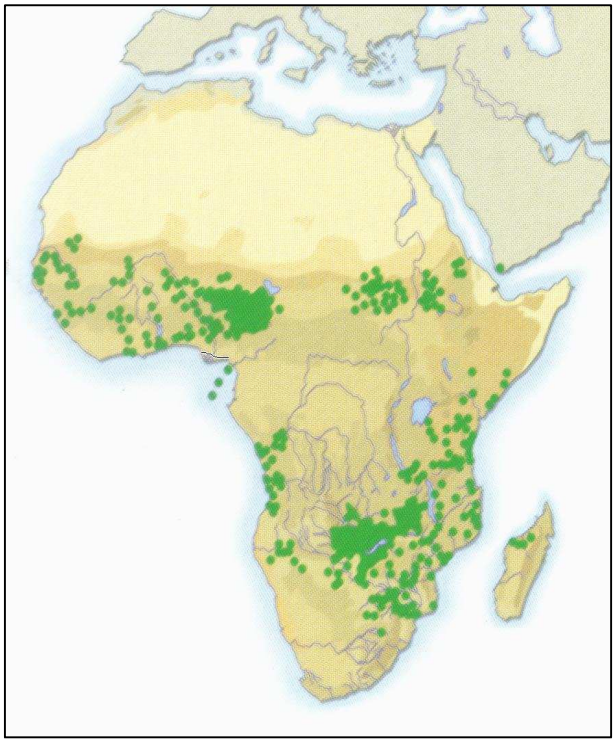

Figure 4. Baobab distribution in Africa. From Wickens and Lowe (2008)

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Chapter 2

Published paper

Baobab (*Adansonia digitata* L.) density, size-class distribution and population trends between four land-use types in northern Venda, South Africa

Citation

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Baobab (*Adansonia digitata* L.) density, size-class distribution and population trends between four land-use types in northern Venda, South Africa

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ABSTRACT

Baobabs are important to people's livelihoods as a source of food, fibre and medicine. Baobab products are increasingly being commercialised and exported around the world, and pressure on the resource is growing (Sidibe and Williams, 2002). This paper examines baobab population structure and trends in northern Venda, South Africa.

We compare the density and life stage data of baobabs in four land-use types (plains, rocky outcrops, fields and villages). Villages and fields had higher densities of trees (2.16 ± 0.44 and 1.13 ± 0.52 plants/ha) than plains and rock outcrops (0.96 ± 0.25 and 0.83 ± 0.24 plants/ha). All land-use types had positively skewed size-class distribution (SCD) curves and negative to flat SCD slopes indicating low recruitment relative to adult density. Villages and fields had the highest juvenile densities, but exhibited flat SCD slopes indicating lowest recruitment relative to mature plant densities. High human numbers, minimal use of baobab fruit and no protection afforded to seedlings, explains low recruitment in villages and fields. Recruitment relative to adult density was most successful in the plains, which exhibited the most positively skewed SCD curves, steepest SCD slopes and the highest percentage of juvenile plants.

Overall, the population is stable with healthy numbers of mature trees. Mortality is very low, and is attributed to the lack of elephants. Quotients and the permutation index suggest that recruitment and mortality is episodic. It is concluded that current levels of recruitment are enough to maintain this population of long-lived trees. Comparisons are made with communal land elsewhere in Africa and neighbouring conservation areas, which exhibit different demographic patterns. This paper serves as a benchmark in the light of demographic changes that may arise from increased commercial use of fruit and a predicted reduction in rainfall due to climate change.

1. Introduction

The baobab (*Adansonia digitata* L. (Malvaceae)) is an iconic tree. Throughout its range the baobab makes an important contribution to people's livelihoods for food, fiber and medicine. Baobab products are bartered and sold in urban and informal markets across Africa. They form an important source of income, especially in the dry season or at times of drought (Sidibe and Williams, 2002). Most recently, general baobab products and, in particular, derivatives of the fruit, such as baobab seed oil and baobab fruit pulp, have been exported to countries outside Africa, mainly Europe, Canada and USA. As baobab extracts become more popular, it is predicted that the demand for these resources will grow (Sidibe and Williams, 2002). To manage these resources sustainably, a thorough understanding of the biology and ecology of the tree is required, along with an understanding of the prevailing socio-economic drivers.

In the Vhembe Municipal District, South Africa, commonly known as northern Venda, commercial use of baobab fruit began in 2005. Fruit is collected from the trees in the communal lands, fields and villages by people (mainly unemployed women). The fruit is processed *in situ* and sold to a locally based company that makes oil from the seeds and packages the fruit pulp. The resulting products are sold to the cosmetic and food ingredients markets. Similar arrangements occur throughout sub-Saharan Africa.

The study of plant population dynamics assesses changes in population size and age distribution. Abundant juveniles relative to adults resulting in an inverse J-shaped size-class distribution curve may be interpreted as a healthy and potentially growing population, but the absence of juveniles indicates a declining population (Condit et al., 1998; Miller, 1998). However, this may not hold for larger, longer-lived species – such as the baobab – where trees can sustain population levels with low or episodic

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recruitment (Condit et al., 1998). In long-lived multi-cohort populations, demographic trends are better described by life-stages than in terms of size-classes. Werner and Caswell (1977) found that stage-related models were better predictors of changes in seed and vegetative reproduction than age-related models.

Baobab populations tend to form bell-shaped or positively skewed size-class distribution curves, with many trees in the middle (100–300 cm dbh) size-classes (Assogbadjo et al., 2005; Chirwa et al., 2006; Dhillion and Gustad, 2004; Edkins et al., 2007; Hofmeyer, 2001). This general lack of recruits in baobabs has led to concern that these populations are vulnerable to severe disturbances such as wild fires, livestock browsing and clearing of fields, which have the potential to cause population collapse (Assogbadjo et al., 2005; Chirwa et al., 2006; Sidibe and Williams, 2002). In parts of Africa where baobab fruit is used in large quantities for domestic purposes and where people protect baobab seedlings, recruitment is better in villages and in fields than in untended areas such as parklands and fallows (Dhillion and Gustad, 2004; Duvall, 2007). Rocky outcrops also provide good areas for baobab recruitment because of seed dispersal by baboons which roost in rocky areas, as well as the protection inaccessible rocky areas afford baobabs from elephants (Duvall, 2007; Edkins et al., 2007; Hofmeyer, 2001; Watson, 2007; Wickens and Lowe, 2008).

This study describes population trends and compares populations in four land-use types (plains, rocky outcrops, fields and villages). We examine the proposition that because baobabs are long-lived trees, with low and episodic mortality (Kelly, 2000; S.M. Venter, unpublished data; Whyte et al., 1996) apparent poor recruitment does not necessarily mean the population is in decline.

2. Materials and methods

2.1. Study site

This research was conducted in northern Vhembe district (northern Venda; 22°19′S and 30°28′E), Limpopo Province, South Africa (Fig. 1). The region has an average altitude of 400 m above mean sea level with gently undulating topography underlain by Karoo Supergroup rocks of the Clarens and Letaba Formations (Brandl, 1981; Mucina and Rutherford, 2006). Soils are generally deep sands and shallow sandy lithosols (Mucina and Rutherford, 2006). Northern Venda experiences semi-arid summer rainfall, characterised by hot summers (October–March) and mild winters (April–September) with mean annual rainfall of between 334 and 423 mm (Mucina and Rutherford, 2006). Annual precipitation is highly variable with a 35–40% coefficient of variation (Schulze, 1997). Frost seldom occurs (Mucina and Rutherford, 2006).

The study area is within the Savanna Biome and comprises Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makulele Sandy Bushveld broad vegetation types (Mucina and Rutherford, 2006). This bioregion unit is dominated by *Colophospermum mopane* (mopane), *Terminalia sericea* (silver terminalia), *Grewia flava* (brandybush) and *Combretum apiculatum* (red bushwillow). The vegetation in general is low sparse woodland with an average tree height of 4–5 m, and a tree cover of 20% (Butt et al., 1994) with emergent baobabs.

Subsistence agriculture and animal husbandry are the main land-use activities between densely inhabited villages. Wooded plains, interspersed with sandstone outcrops are used mainly for grazing cattle, goats and donkeys. Subsistence crops are grown in the wet season (dryland cropping). There is open access to these natural resources with minimal control from traditional institutional structures and government. Bush fires are not common due to low grass and herb biomass, and elephants are infrequent visitors. The 2001 population census estimated a density of approximately 200 people/km^2. The ratio of men to women is 1:4 with a 0.78–2.38% level of formal employment (Statistics-S.A., 2001).

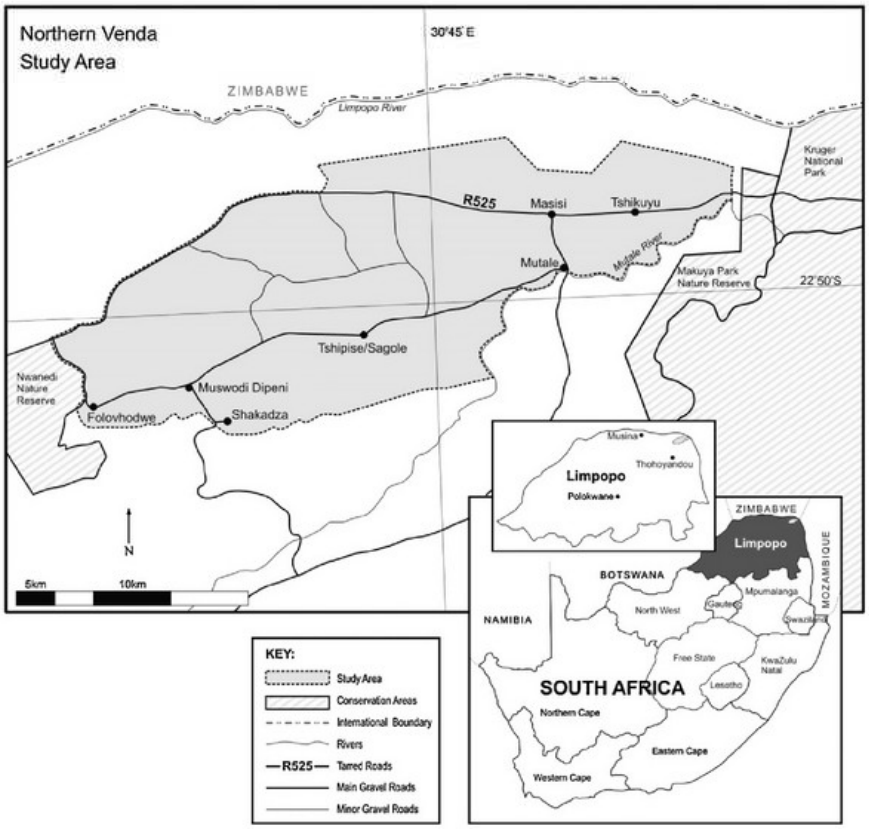

Fig. 1. Map indicating location of Northern Venda study area in Limpopo Province, South Africa.

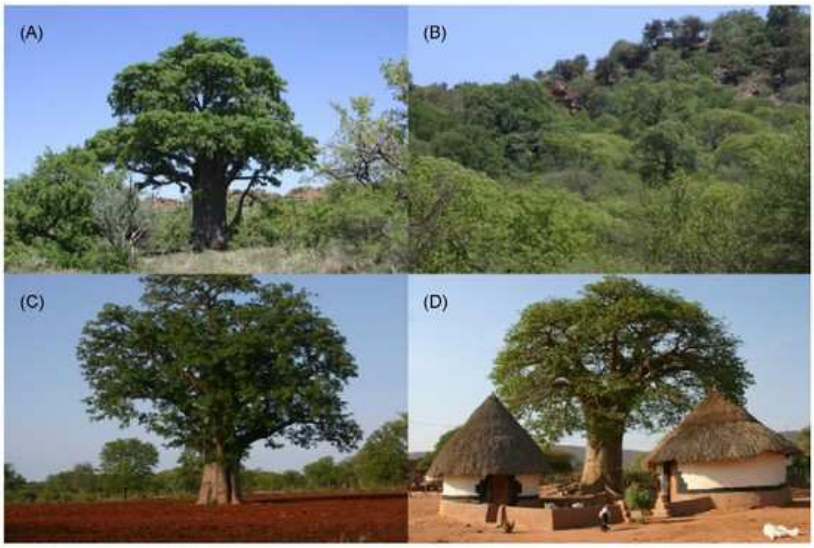

Fig. 2. Photographs of the four land-use types which were compared during the study. (A) plains, (B) rocky outcrops, (C) fields, (D) villages.

2.2. Study species

Adansonia digitata is one of the eight species of baobab in the genus *Adansonia* L. (Malvaceae, subfamily Bombacoideae) and the only one that occurs on mainland Africa (Baum, 1995). It is present throughout most of Africa, south of the Sahara. In South Africa the population is limited to the Limpopo River valley, with the exception of a few isolated trees found further south (Wickens and Lowe, 2008).

Baobabs generally inhabit a wide range of well-drained soils (clays to sands) in the drier plant communities of the Sudanian and Zambezian lowlands where rainfall is 200–800 mm annually (Wickens, 1982; Wickens and Lowe, 2008). They are often found along seepage lines and on the crests of rock outcrops (Wickens and Lowe, 2008). In southern Africa baobabs are emergents, associated with *Colophospermum* (mopane), *Cordyla* (wild mango) and *Kigelia* (sausage tree) woodlands in low-lying, dry, hot and generally frost-free areas (Wickens, 1982; Wickens and Lowe, 2008). Baobabs are deciduous in the dry season. Flowering lasts for two to three months during the wet season and coinciding with early leaf production (Baum, 1995; Wickens, 1982).

Baobab fruits are large, +12 cm in length (Palgrave, 1983). The pericarp is woody and indehiscent. Seeds are distributed by humans and animals, like baboons, chimpanzees and elephants (Wickens and Lowe, 2008). Baobabs are known to be extremely long-lived trees, despite the softness of their wood. Age estimates vary between 1000 and 2000 years (Wickens, 1982).

2.3. Sampling and measurement

Trees were sampled in October and November 2006. Four land-use types were sampled: (1) plains; (2) rocky outcrops; (3) fields and (4) villages (Fig. 2). Six sample sites were randomly selected from maps for each of the four land-use types. Sites were sampled using strip transects 1 km long × 50 m wide (i.e. 5 ha). Village plots were the exception with 0.5 km long transects. This was done to accommodate small villages. The number of transects done in each land-use type was determined by their relative sizes: plains had 48 transects (48 ha × 5 ha = 240 ha); rocky outcrops had 24 transects (24 ha × 5 ha = 120 ha); Fields had 12 transects (12 ha × 5 ha = 60 ha) and villages had 12 transects (12 ha × 2.5 ha = 30 ha).

All baobab trees in the transects were measured. Diameter at breast height (DBH) was measured. Height for each tree was estimated to the closest 2 m (i.e. 2, 4, 6, ...m). Baobab saplings (DBH < 1 cm) were counted. Dead and decomposing trees were recorded.

2.4. Data and statistical analysis

Diameter at breast height (DBH) was used and is reported here. However, we also analysed mean girth so that comparisons could be made with a similar analysis by Edkins et al. (2007) in the Kruger National Park.

2.4.1. Population density per land-use type

Tree numbers were converted into densities (plants/ha), and girth to diameter. Statistica 7 was used for univariate analyses. Analysis of Variance (ANOVA) followed by Fisher's Least Significant Difference (LSD, $p < 0.05$) test was used to compare baobab densities across the land-use types.

2.4.2. Size-class distributions

ANOVA was used to compare girth at breast height (gbh) between land-use types (following Edkins et al., 2007). To allow for visual comparisons, size-class distributions (SCDs) were constructed and displayed graphically. Size-classes were determined as 50 cm increments in diameter at breast height (dbh), i.e. 0–49 cm, 50–99 cm, 100–149 cm, ..., ≥500 cm dbh. Kolmogorov–Smirnov tests were used to compare size-class distributions and to test the prediction that all size-classes occurred in similar proportions among land-use types.

2.4.3. Population trends

Trees were divided into juveniles (≤99 cm dbh generally not yet producing fruit) and mature (≥100 cm dbh-producing fruit), based on fruit production per tree size-class (SM Venter, unpublished data). A senescent category was not defined because there is no significant reduction of fruit production in large trees (SM Venter, unpublished data). Percentages and densities of mature and juvenile plants are reported for each land-use type. ANOVA followed by Fisher's LSD was used to compare the density of juvenile and mature populations between land-use types. Paired *t*-tests were used to compare juvenile and mature tree densities within each land-use type and across the whole population. Using a chi-square contingency table, mature and juvenile population sizes within the four land-use types were compared.

Size-class distribution (SCD) slopes for each land-use type were calculated using the method described in Condit et al. (1998) and Lykke (1998). SCD slopes were used as indicators of population structure (Mwavu and Witkowski, 2009; Obiri et al., 2002). A least-squares linear regression was performed on the SCD data, with size-class midpoint (ln transformed) as the independent variable and the average number of individuals per size-class ($\ln(N_i+1)$) as the dependent variable. The interpretation of the SCD slopes is based on those described by Obiri et al. (2002): negative slopes indicate good recruitment, with more individuals in smaller size-classes than in larger size-classes; flat slopes indicate equal numbers of individuals in small and large size-classes; and positive slopes indicate poor recruitment with more trees found in larger than in smaller size-classes. Steepness of the slope was used to further describe recruitment trends. Steep negative slopes indicate better recruitment than shallow slopes (Lykke, 1998; Mwavu and Witkowski, 2009; Obiri et al., 2002).

Population stability was examined by calculating quotients between successive size-classes and displaying the results graphically. Constant quotients between successive size-classes indicate a stable population, while fluctuating quotient values are an unstable population (Botha et al., 2004; Shackleton, 1993).

The Permutation Index (P) was developed by Wiegand et al. (2000) to measure the degree of deviation from the monotonic decline expected in an undisturbed population. Size-classes are ranked from smallest (most frequent) to largest (least frequent). A monotonically declining population will have a Permutation Index = 0 and a population with a discontinuous SCD will have a permutation index > 0.

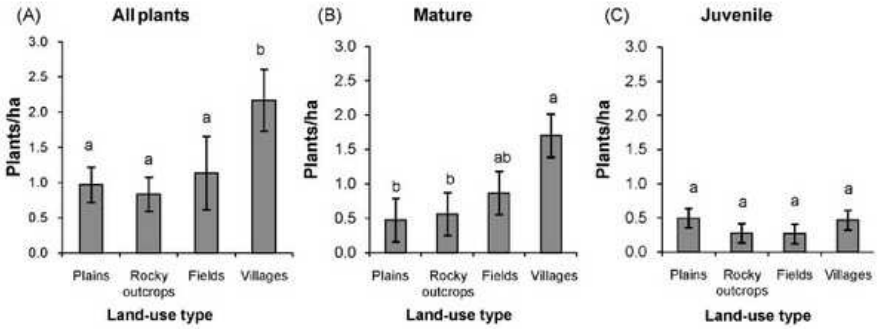

Fig. 3. Density (mean ± SE) of all plants (A), mature (B) and juvenile (C) baobab populations in different land-use types. Bars marked with different letters (a and b) are significantly different (Fisher's LSD, $p < 0.05$).

3. Results

3.1. Population density per land-use type

The density of the baobab population across all land-use types was 1.03 ± 0.21 (S.E.) plants/ha. Villages had slightly higher densities of trees than all other land-use types ($F_{3,20} = 2.5309$, $p = 0.0860$), followed by fields, plains and rocky outcrops (Fig. 3).

3.2. Size-class distributions

The SCD for the whole population and the populations of baobab trees in each land-use type had positively skewed distribution curves, with most trees in the 50–200 cm dbh size-classes (Fig. 4). Plains have the most positively skewed SCD curve and Kolmogorov–Smirnov comparisons confirmed that it was significantly ($p < 0.05$) different to the SCD curves in other land-use types. The mean girth

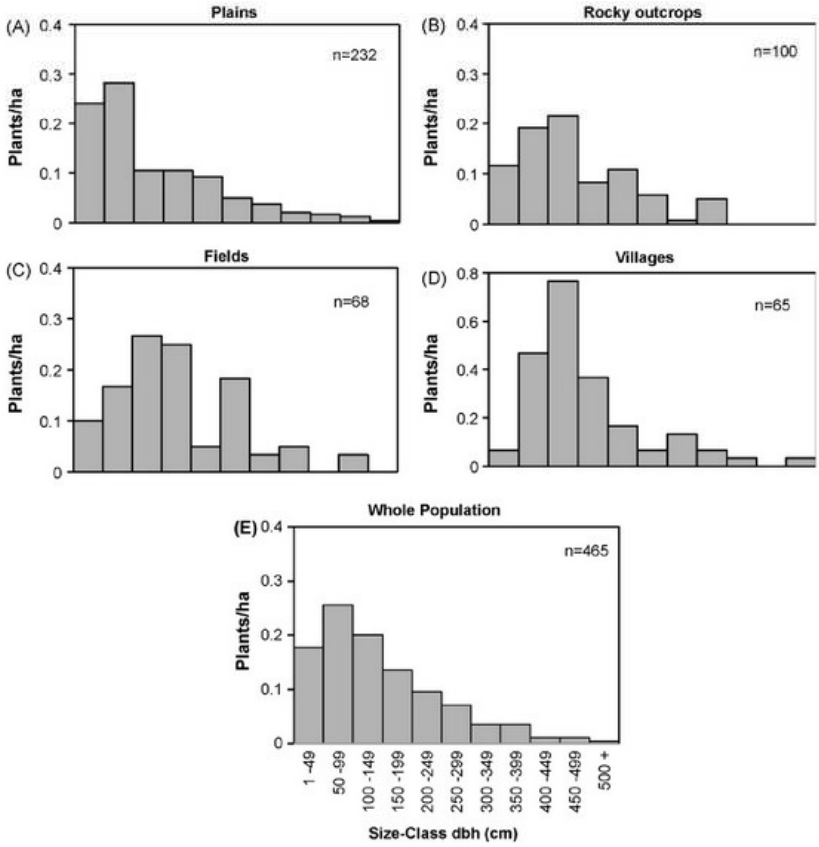

Fig. 4. Size-class distributions (dbh in 50 cm intervals) for each land-use type: plains (A), rocky outcrops (B), fields (C), villages (D) and for the whole population (E). Note Y-axis of villages (D) double the length of other figures.

Table 1
Percentage juveniles, slope of regression (dbh versus number of individuals), and Permutation Index (P) for the whole population and for different land-use types.

Land-use type	%	SCD slope				Permutation Index
	Juveniles	Slope (°)	r^2	t	p	P
Whole population	39%	−0.38	0.75	−5.13	<0.001	6
Plains	51%	−0.28	0.88	−7.96	<0.001	3
Rocky outcrops	33%	−0.12	0.55	−3.33	<0.01	11
Fields	24%	−0.06*	0.26	−1.78	>0.05	21
Villages	22%	−0.05*	0.18	−1.42	>0.05	16

* Flat slope.

at breast height (gbh) of the land-use types were not significantly different.

3.3. Population trends

Plains have the highest percentage of juveniles followed by Rocky outcrops, fields and villages (51%, 33%, 24%, and 22% Table 1). The population as a whole had 39% juveniles (Table 1). The density of juveniles was similar between land-use types with plains and villages having slightly higher densities than rocky outcrops and fields (Fig. 3). The density of mature plants was significantly higher in villages, ($F_{3,20} = 3.1772$, $p = 0.0464$) followed by fields, rocky outcrops and plains (Fig. 3).

Paired t-tests comparing the densities of mature and juvenile plants within each land-use type found significant differences in rocky outcrops and villages ($p < 0.05$), but not in plains and fields (Fig. 5). Chi-squared contingency table confirmed significantly different abundances of mature and juvenile trees among the four land-use types ($X_3^2 = 31.38$, $p < 0.0001$). Regional density of juveniles (0.38 ± 0.07 plants/ha) was significantly lower ($p < 0.05$) than the regional density of mature plants (0.90 ± 0.18 plants/ha; Fig. 5).

SCD slopes were negative for plains and rocky outcrops, indicating that there were more individuals in smaller size-classes than in larger size-classes (Table 1). Plains had the steepest slope, i.e. the best recruitment-followed by rocky outcrops. Fields and villages had the flattest slopes with close to equal numbers of plants in small and large size-classes, indicating lowest recruitment.

Quotients calculated between successive size-classes indicated that the populations of baobab trees in all land-use types were not evenly distributed (Fig. 6). Quotients calculated for the population as a whole masked much of this variation, showing a more even distribution in the smaller size-classes and an uneven distribution in the larger size-classes.

The Permutation Index for the regional population as well as for populations in different land-use types was greater than zero (Table 1) suggesting that recruitment and mortality are episodic events.

No dead or decomposing baobab trees were found.

4. Discussion

4.1. Trends at land-use level

Our study has revealed a number of important patterns and contrasts at the land-use level. Differences in the demographic patterns exhibited by plains and villages are particularly noteworthy. Villages had a significantly higher density of trees than plains (Fig. 3) and yet they had similar densities of juveniles (Fig. 3). Paired t-tests confirmed significantly lower densities of juveniles to mature trees in villages, and not in plains (Fig. 5). This shows that adult trees in villages did not recruit as successfully as those in plains. Further statistical analyses confirmed that recruitment success, relative to adult populations, in plains was better than in villages. The SCD curve in plains was more positively skewed than in villages (Fig. 4), which was confirmed by Kolmogorov–Smirnov tests, and SCD slopes were steeper in plains indicating better relative recruitment (Table 1). Quotients showed a more stable population (Fig. 6) and the permutation index was lower in plains (Table 1).

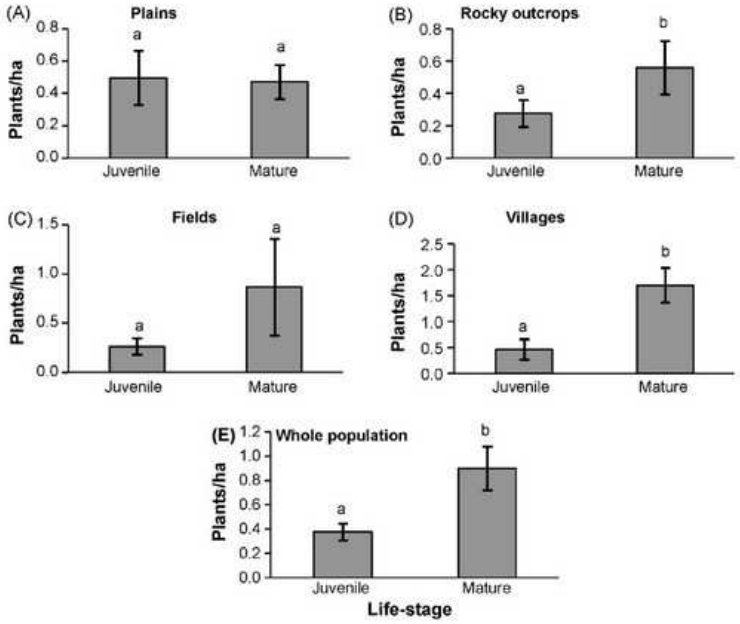

Fig. 5. Density of juvenile versus mature baobabs (mean ± SE) in plains (A), rocky outcrops (B), fields (C), villages (D) and whole population (E). Bars marked with different letters (a and b) are significantly different (Fisher's LSD, $p < 0.05$). Note different Y-axis scales.

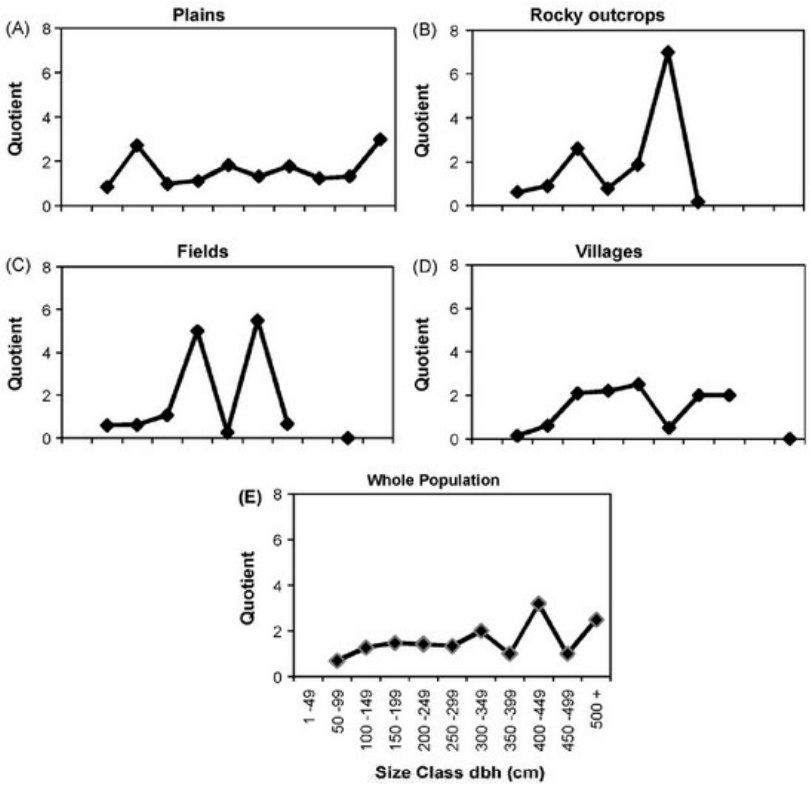

Fig. 6. Quotients between density of baobabs in successive size-classes (dbh in 50 cm intervals) for plains (A), rocky outcrops (B), fields (C), villages (D) and whole population (E).

In contrast, studies in West Africa have found that high baobab density and good recruitment is often associated with human settlement and activity (Assogbadjo et al., 2005; Dhillion and Gustad, 2004; Duvall, 2007). Duvall (2007) reports that the Manika-speaking people of West Africa effectively disperse baobab seed by collecting and using large quantities of fruit, the seeds of which are discarded around villages, where they germinate. There is also a culture of actively protecting seedlings from livestock thus increasing recruitment success of baobabs near human habitation (Assogbadjo et al., 2005; Dhillion and Gustad, 2004; Duvall, 2007). In West Africa, low recruitment rates in plains (fallows), are attributed to livestock browsing and trampling, clearing new fields, digging up seedlings to eat tap-roots, fire and overharvesting of fruit and leaves (Assogbadjo et al., 2005; Chirwa et al., 2006; Dhillion and Gustad, 2004). Our data shows that plains have a more stable population than villages with better recruitment relative to adult populations. In Northern Venda the population of trees in plains is widely spread with less exposure to disturbances caused by human activity. High human densities, infrequent domestic use of baobab fruit and lack of seedling protection may have a negative effect on recruitment in villages. The people in West Africa appear to have a stronger 'baobab culture' than the people in northern Venda which may be the reason for the difference between the two areas.

In the neighbouring Kruger National Park, density and recruitment of baobabs in plains is lower than on rocky outcrops (Edkins et al., 2007; Hofmeyer, 2001; Kelly, 2000). In contrast our data showed higher densities of baobabs and better recruitment on plains than on rocky outcrops. In the Kruger National Park elephants have a major impact on baobabs, rocky outcrops are often inaccessible to elephants and thus act as refuge sites (Edkins et al., 2007). Both the present lack of elephants in northern Venda and the impact of baboons on seed production in rocky outcrops (SM Venter, unpublished data) may explain why the baobab population is distributed differently in northern Venda compared to the Kruger National Park.

4.2. Trends in baobabs at a population level

The classic inverse J-shaped SCD is generally used by biologists as an indication of a healthy, regenerating population, deviation from this would normally be a cause of concern (Wilson and Witkowski, 2003). Therefore, low recruitment rates and bell-shaped or positively skewed size-class distributions, which are typical of baobab populations across Africa (Assogbadjo et al., 2005; Chirwa et al., 2006; Wilson, 1988) has led many authors to express concern about the maintenance of baobab populations (Assogbadjo et al., 2005; Chirwa et al., 2006; Wickens and Lowe, 2008). However, due to the long-lived nature of baobabs and extremely low adult mortality rate, low recruitment rates may not be a cause for concern.

A number of authors have pointed out that baobab recruitment is often underestimated because of the false predictions made about baobab growth rates. Dhillion and Gustad (2004) argued that the direct conversion of girth to age underestimates baobab recruitment, as young baobabs grow faster relative to older trees,

suggesting that recruitment is not as poor as it appears. Breitenbach and Breitenbach (1985) analyzed the growth of 40 planted baobab trees of known age, and found that baobab tree growth tapers off within the first quarter of the lifespan of the tree (after 200 years of an 800-year old tree); thus three quarters of its life (±600 years) is spent at almost the same diameter. They too warned that the extremely slow growth of adult trees could lead to false predictions of baobab ages. This was supported by Patrut et al. (2007), who did radiocarbon dating of the 'Grootboom' (meaning big tree) baobab in Namibia.

Condit et al. (1998) confirm that trees which grow rapidly in small size-classes and trees that have a high overall rate of survival will exhibit flat SCD slopes, and also that large, long-lived trees are able to sustain population levels with low or episodic recruitment. Wickens and Lowe (2008) also pointed out that, because of the longevity of baobabs, only a few recruits are necessary to maintain the current population of trees. Hofmeyer (2001), came to the same conclusion in the Kruger National Park, 20 km east of our study site. She has suggested that there are sufficient trees in reproductive size-classes, and that the low number of small trees simply indicate a poor recruitment phase for baobabs.

During our surveys we did not come across any dead or decomposing baobabs. Interviews with villages confirmed that mortality has been very low for many years and that baobabs only die in bad droughts (SM Venter, unpublished data). Kelly (2000) and Wilson (1988) calculated baobab annual mortality rates from populations across Africa and obtained mortality rates of between 0.69 and 3.7%. Whyte et al. (1996) found that baobab mortality was strongly linked to elephant numbers and that drought caused episodic baobab mortality.

Despite the acceptability of low recruitment rates for baobabs, Wickens and Lowe (2008) were of the opinion that baobabs may currently be threatened by climate change because regeneration appears to be confined to areas with higher rainfall. This concern was also expressed by Maranz (2009) who found that ecosystems in the African Sahel are losing large trees due to changing climate patterns.

Our conclusion is that the baobab population in northern Venda is currently stable. Our data indicates a population that has a healthy proportion of mature trees in all land-use types. The lack of elephants in the area explains low mortality rates. Although SCD curves are not typically inverse J-shaped (normally associated with good recruitment), baobabs are very long-lived trees so that even with low recruitment, current population levels can be maintained. Our data indicates that recruitment (specifically seedling establishment) and mortality are very likely to be episodic events. More information is required on factors that trigger these events.

However, recent expansion of baobab fruit harvesting and the predicted drop in rainfall attributed to climate change may negatively affect future recruitment and may increase tree mortality. Thus knowledge of current recruitment and mortality rates will guide resource management decisions and serve as a valuable reference point in future population studies. In villages, where baobab populations have relatively low recruitment rates, resource managers should encourage a 'culture' that will enhance regeneration.

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Chapter 3

Paper in press

Baobab (*Andansonia digitata* L.) population dynamics between vegetation and soil types and natural and human-modified landscapes in northern Venda, South Africa.

Paper presented at the Fifth Natural Forests and Woodlands Symposium, Richards Bay April 2011

Abstract

Across their distribution, Baobabs (*Adansonia digitata* L.) are found in a wide variety of vegetation and soil types. Baobabs are also associated with human-modified landscapes where adult trees are often protected by local people. Despite this, little is known on how the structure of baobab populations differ between (a) vegetation types, (b) soil types and (c) between natural and human-modified landscapes. This study investigated variations in population density and size- and life stage class distributions of baobabs in a communally managed area in South Africa. Baobabs in this region are associated with *Grewia*, *Commiphora* and *Colophospermum mopane* dominated vegetation, the latter two genera, in particular are associated with arid savannas. Of the three vegetation types found in the area, Makuleke Sandy Bushveld had the highest density of baobabs (1.43 ± 0.31 plants/ha) followed by Limpopo Ridge Bushveld (0.86 ± 0.15 plants/ha) and Musina Mopane Bushveld (0.77 ± 0.10 plants/ha). Sandstone derived soils had higher densities of baobabs (1.21 ± 0.14 plants/ha) than soils derived from basalts (0.34 ± 0.09 plants/ha) and aeolian (0.59 ± 0.09 plants/ha) deposits. Makuleke Sandy Bushveld had higher densities of sub-adults relative to adults than Musina Mopane Bushveld and Limpopo Ridge Bushveld. Sub-adult density was higher than adult density in basalt derived soils and lower in sandstone and aeolian derived soils. Size-class distributions did not differ between vegetation types or between soil types. The density of trees in human-modified landscapes (villages and fields) (1.65 ± 0.36 plants/ha) was almost twice as high as in natural landscapes (0.90 ± 0.17 plants/ha). However human-modified landscapes had bell-shaped size-class distribution curves and significantly lower densities of sub-adults relative to adults which indicate that current management practices in these areas are hampering recruitment.

Key words

Communal lands, density, geology, life stage, regeneration, size-class distribution, savanna, soil, vegetation.

1. Introduction

Throughout their range baobabs are associated with a wide variety of vegetation and soil types (Barnes, 1980; Assogbadjo *et al.*, 2005; Chirwa *et al.*, 2006). Baobabs reach the southern limit of their distribution in the northern part of South Africa. Here baobabs are distributed along the Limpopo river valley from Lephalale to Pafuri. However isolated individuals are found south of the Olifants River in Klaserie Private Nature Reserve; these may have been dispersed by humans hundreds of years ago (Witkowski, 1983).

In South Africa, baobabs are broadly found within the Mopane and Lowveld Ecoregions, and at a finer scale within Musina Mopane Bushveld, Limpopo Ridge Bushveld, Cathedral Mopane Bushveld, Makuleke Sandy Bushveld and Subtropical Alluvial Vegetation (Mucina and Rutherford, 2006). These are broad scale (1:1 000 000) vegetation units, but within these units there is considerable variation in vegetation and associated underlying geology and soils.

Baobabs are important for many rural people in Africa, because they are revered for their spiritual presence and provide products on which people rely, such as food, fiber and medicine. For this reason, baobabs are often protected and adult trees are seldom cut down (Sidibe and Williams, 2002). Despite this, there is growing concern about the persistence of baobabs in many landscapes (Dhillion and Gustad, 2004; Chirwa *et al.*, 2006).

Baobab populations, across a number of land-use types in northern Venda were evaluated at broad spatial scales by Venter and Witkowski (2010), but there is considerable unexplained variation at finer scales within these land-use types. In order to shape our understanding of populations in both natural and human-modified environments, demographic factors associated with baobab populations at a finer scale need to be understood.

The aim of this study was to describe the structure of baobab populations in different vegetation and soil types and to compare between natural and human-modified environments. This was done by comparing (a) plant density, (b) size class distributions (SCDs) and (c) the relative abundance of sub-adults to adults in each case.

The key questions asked were:

1. How do baobab populations differ between vegetation and soil types?
2. Is recruitment in human-modified landscapes lower than in natural landscapes?

2. Materials and Methods

2.1 Study site

Research was conducted in the northern part of Limpopo Province, South Africa. The area is commonly referred to as ‘northern Venda’ (centring on 22°50’S and 30°45’E) (Fig. 1). It lies at an average altitude of 400m above mean sea level with gently undulating topography (Brandl, 1981). The area is semi-arid with hot summers (October-March) and mild winters (April–September) with mean annual summer rainfall of between 334 and 423 mm (Mucina and Rutherford, 2006). Frost seldom occurs, bush fires are rare and elephants are infrequent visitors (pers. obs.).

The area falls within the Savanna Biome and is comprised of the following broad vegetation types: Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makulele Sandy Bushveld within the Mopane and Lowveld Ecoregions (Mucina and Rutherford, 2006). Musina Mopane Bushveld forms moderately closed to open shrubveld to open savanna with a well developed field layer and poorly developed herbaceous layer. Limpopo Ridge Bushveld is a moderately open savanna with a poorly developed ground layer. Makuleke Sandy Bushveld is a tree savanna occurring mostly in the south eastern part of the study area. Karoo Supergroup rocks of the Clarens and Letaba formations and basalts underlie the area.

The land is communally managed and the local BaVenda people depend on livestock grazing and subsistence agriculture for their livelihoods. Natural vegetation in villages and fields has mostly been cleared except for wild fruit trees such as *Sclerocarya birrea* subsp. *caffra* (marula), *A. digitata* (baobab) and *Berchemia zeyheri* (red ivory).

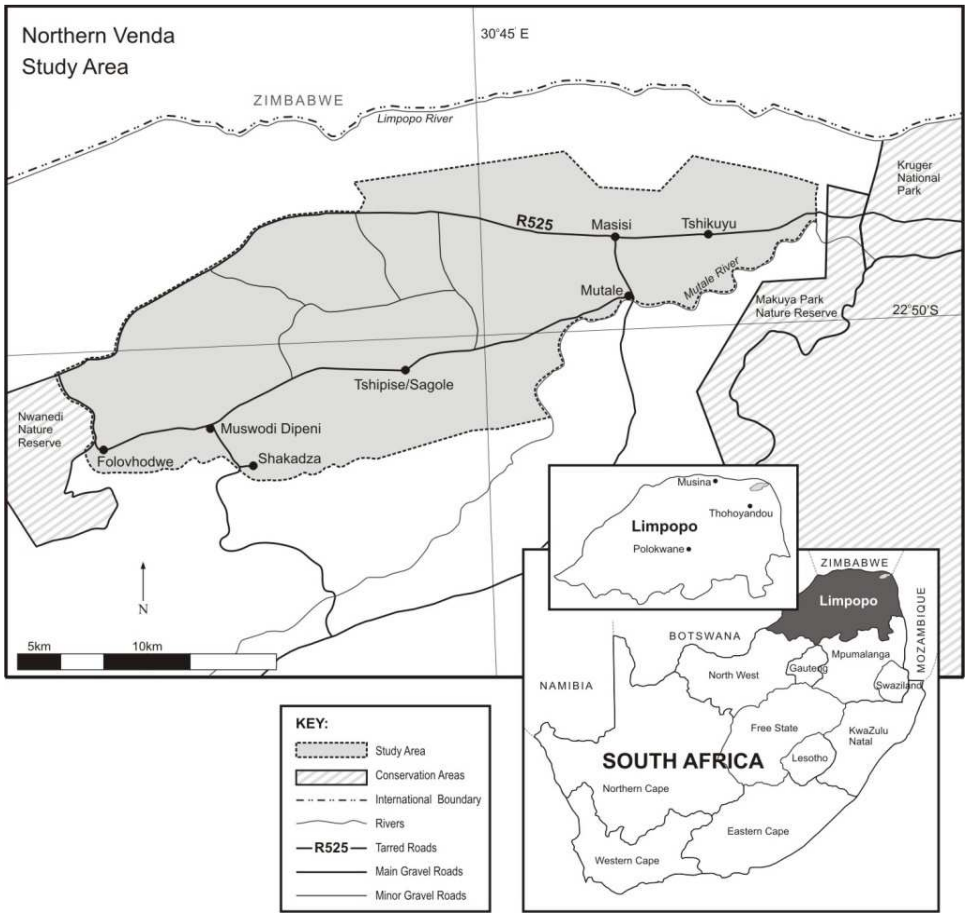

Figure 1. Map indicating location of study area in Limpopo Province, South Africa.

2.2 Study species

Adansonia digitata is one of eight species of baobab in the genus *Adansonia* L. (Malvaceae, subfamily Bombacoidea) (Baum, 1995b). Baobabs are characteristic of the Sudano-Zambesian lowlands with 200 – 800 mm annual rainfall. In Southern Africa baobabs are found in *Colophospermum mopane* woodands and *Cordyla africana* and *Kigelia africana* savannas. They are found on a variety of substrates from heavy-textured soils to deep well-drained sands (Wickens, 1982).

Saplings and seedlings have simple leaves and an underground carrot-like tuber that acts as a food reserve until the tree is larger. Young trees are steeply tapered with few branches. Later the tree thickens and the trunk is more or less uniform in diameter. Adult trees are characterized by their massive size, stout trunks and wide spreading crown (Wickens, 1982). Trees are known to be extremely long-lived and age estimates of large trees reach 1300 years (Patrut *et al.*, 2009).

Baobabs are deciduous, producing leaves in the rainy season. Young leaves are 2-3 foliate and become 5-7 foliate once matured (Baum, 1995a). Flowering usually lasts 4-6 weeks with a few flowers opening each night (Baum, 1995a). Trees produce large capsule-like fruit which mature during the dry season. Seeds are imbedded in a dry, mealy pulp within the fruit (Wickens, 1982). In Southern Africa adult trees produce an average of 77 fruit per tree per year (Venter and Witkowski, 2011).

2.3 Sampling and measurement

Field work was done in October and November 2006. Using 1:50 000 topographical maps and a co-ordinate overlay grid, randomly generated numbers enabled sample sites to be identified. Sampling was done in plots measuring 5 ha (50m x 1km) each, except for plots in villages which measured 2.5 ha (50m x 0.5km) each. Seventy two plots (360 ha) were located in natural landscapes and 24 (90 ha) in human modified areas. These are atypical and very large areas precisely because baobabs are the largest trees in these landscapes and large areas need to be covered to obtain meaningful samples.

All baobab trees in transects were measured. Girth measurements were taken at 1.3m above the ground using a fibreglass tape measure. Height for each tree was estimated to the closest 2m (i.e. 2, 4, 6, ...m). If any saplings (dbh < 1cm) were found, these would have been counted.

Transects in natural landscapes were classified into the three broad vegetation units of Mucina and Rutherford (2006). These were further divided into ten fine-scale vegetation types based on dominant species. Five soil types were described by colour and texture of soil and these were grouped into three parent material types from which these soils were

derived: sandstone, basalt and aeolian. Vegetation and soil type descriptions were not done for human-modified landscapes as these areas had been cleared of natural vegetation and their soils disturbed by human activities.

2.4 Data and statistical analysis

2.4.1 Population density

Fine scale vegetation and soil types represented subtypes of the broad scale vegetation and soil (parent material) types. Density (plants/ha) was calculated for each fine and broad scale vegetation and soil type. These were compared using ANOVA, followed by Fisher's LSD. Density data for fine scale vegetation types were square-root transformed before analysis. Density of plants in the natural landscape as a whole was compared to the adjacent human modified landscape using a t-test.

2.4.2 Size-Class distributions (SCD)

Size-class distributions (SCD) were constructed for each broad scale vegetation type, parent-material type and for the natural landscape as a whole. Using data from Venter & Witkowski (2010), a SCD for the human modified landscape (villages and fields) was also constructed and compared to that of the natural landscape. Size-classes were determined as 50 cm increments in diameter at breast height (dbh), i.e. SC1: 0–49cm; SC2: 50–99cm; SC3: 100–149cm and so on up to ≥500cm dbh. Kolmogorov-Smirnov tests compared size-class distributions using R (RDevelopmentCoreTeam, 2010).

2.4.3 Life stages

Trees were divided into sub-adults (<99cm dbh i.e. not yet producing fruit) and adults (≥100cm dbh i.e. producing fruit), based on fruit production per tree size-class (Venter and Witkowski, 2011). ANOVA followed by Fisher's LSD was used to compare the density of sub-adult and adult populations between vegetation types and soil parent material types. Paired t-tests were used to compare sub-adult and adult tree densities within each vegetation and soil parent material type and between natural and human modified landscapes. The percentages of sub-adults were reported.

Size Class Distribution slopes were calculated using the method described in Condit *et al.* (1998) and Lykke (1998). These were used to indicate recruitment trends: negative slopes indicate good recruitment, with more individuals in smaller size-classes than in larger size-classes; flat slopes indicate equal numbers of individuals in small and large size-

classes; and positive slopes indicate poor recruitment. Steep negative slopes indicate better recruitment than shallow slopes (Lykke, 1998; Obiri *et al.*, 2002; Mwavu and Witkowski, 2009).

3. Results

3.1 Population densities

There were significant differences in the densities of baobabs between broad-scale vegetation types ($F_{2,69}$=3.9022, p=0.0248) with Makuleke Sandy Bushveld having significantly higher densities than Musina Mopane Bushveld (Fig. 2).

There were also significant differences in baobab densities between local vegetation types ($F_{9,62}$=7.0498, p<0.001) (Fig. 2). Vegetation dominated by *Commiphora/Grewia* (LVT7) had significantly higher densities of baobabs than all other vegetation types, except for the *Terminalia*/*Colophospermum* (LVT9) woodlands. *Colophospermum*/*Aloe* thickets (LVT1) had the lowest densities of baobabs and was significantly lower than all other vegetation types except those with *Terminalia* as one of the dominant trees (LVT8,9 &10).

Baobab densities were also significantly different between parent-material types ($F_{2,69}$=9.0356, p=0.0003). Density was higher on soils derived from sandstones than on soils derived from basalt and aeolian deposits (Fig. 3).

Densities of baobab trees in the five different soil types also showed significant differences ($F_{4,67}$=4.6588, p=0.0022) (Fig. 3). The density of baobabs in light sandy soil was significantly higher than in dark stony soil, dark sandy soil and red sandy soil.

Human modified landscapes tended to have higher densities of trees (1.65 ± 0.35 plants/ha) than natural landscapes (0.90 ± 0.17 plants/ha) (t_{22} = -1.8928, p=0.0716).

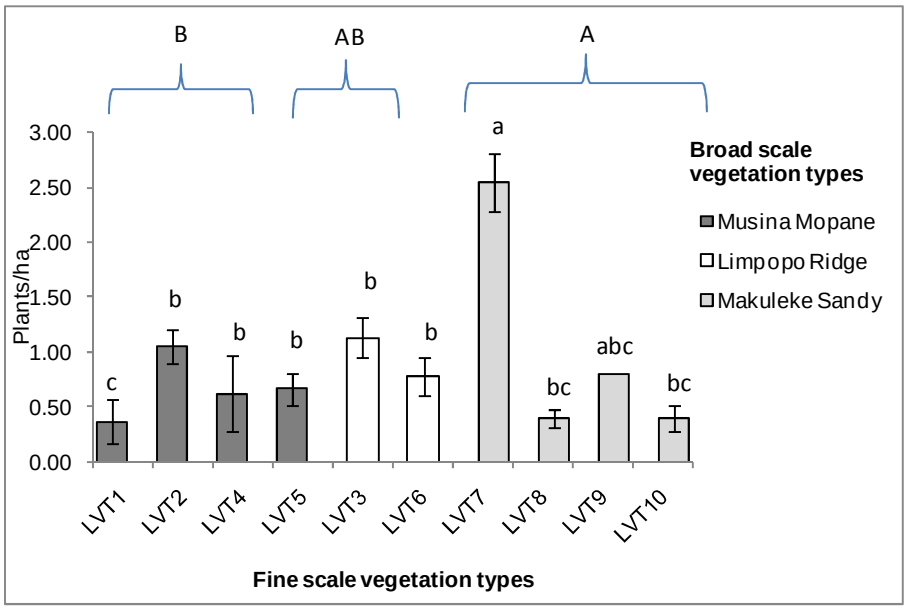

Figure 2. Broad scale and fine scale baobab density per vegetation types in natural landscapes. Broad scale density shown by Musina & Rutherford (2006) bushveld types: Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makuleke Sandy Bushveld. Bars grouped by brackets (A,B) show significant differences between Bushveld types (Fishers LSD, $p<0.05$). Fine scale density shown by local vegetation types (mean ± SE): LVT 1 - Colophospermum-Aloe, LVT2 - Colophospermum-Commiphora-Boscia-Acacia-Grewia, LVT3 - Colophospermum-Commiphora-Kirkia, LVT4 - Colophospermum-Sclerocarya-Grewia-Boscia, LVT5 - Androstachys-Colophospermum, LVT 6 - Adrostachys-Commiphora-Acacia-Terminalia-Kirkia-Croton, LVT7 - Commiphora-Grewia, LVT 8 - Terminalia-Sclerocarya-Boscia, LVT9 - Terminalia-Colophospermum, LVT10 - Commiphora-Terminalia. Bars marked with different letters (a,b,c) are significantly different (Fishers LSD, $p<0.05$).

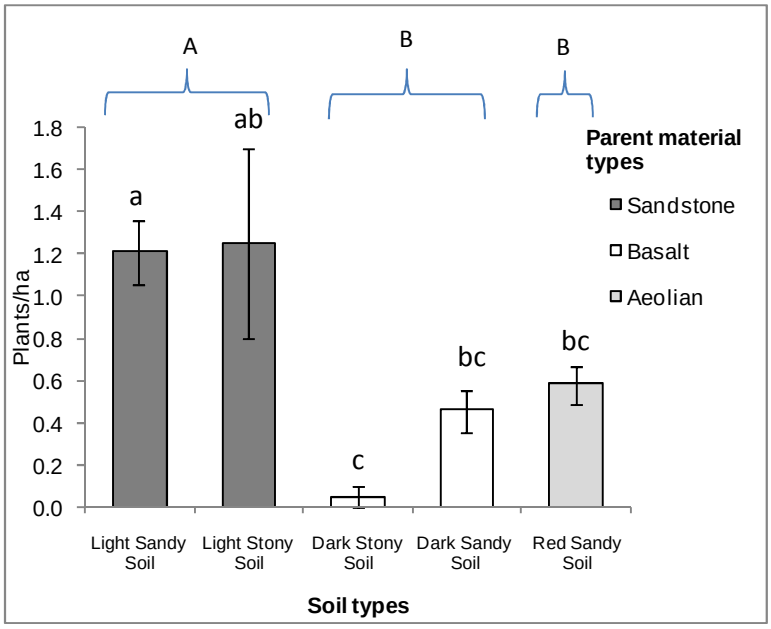

Figure 3. Baobab density per soil type (mean ± SE) and grouped by parent-material types in natural landscapes. Bars marked with different letters (a,b,c) show significant differences in soil types (Fishers LSD, $p<0.05$). Grouped bars indicated by brackets and marked with different letters (A,B) indicate significant differences in parent material types (Fishers LSD, $p<0.05$).

3.2 Size-Class Distributions

The size-class distributions for the populations of baobab trees in Musina Mopane Bushveld and Limpopo Ridge Bushveld were inverse J-shaped, with the majority of trees falling in the three smallest dbh size-classes (Fig. 4). Makuleke Sandy Bushveld had a positively skewed curve with fewer plants in the smallest dbh class than in the next two larger size-classes. Kolmogorov-Smirnov comparisons showed that the SCD curves of the three vegetation types were not significantly different ($p > 0.05$).

Sandstone was by far the predominant substrate in the study region (80% of trees). Size-class distributions on sandstone and aeolian derived soils were positively skewed and inverse J-shaped for basalt derived soils. (Fig. 5). However, Kolmogorov-Smirnov comparisons indicated that the SCD curves of the three soil parent-material types are not significantly different ($p > 0.05$), but this may be an artefact of low numbers of trees sampled on basalt and aeolian derived soils.

A Kolmogorov Smirnov test also showed that the natural and human-modified landscape SCDs did not differ significantly ($p > 0.05$) (Fig. 6).

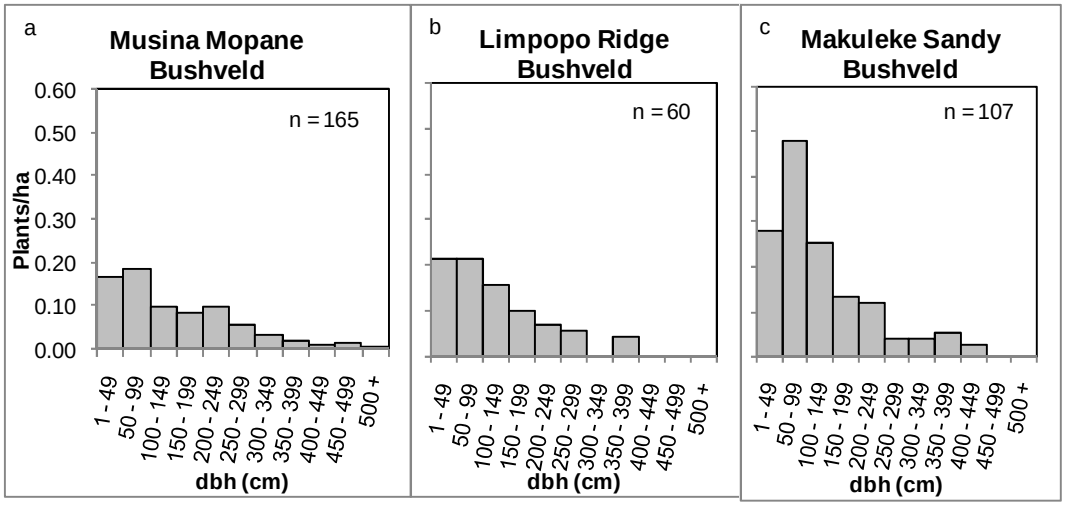

Figure 4. Size-class distribution (50cm dbh intervals) per broad scale vegetation type in natural landscapes: Musina Mopane Bushveld (a), Limpopo Ridge Bushveld (b) and Makuleke Sandy Bushveld (c).

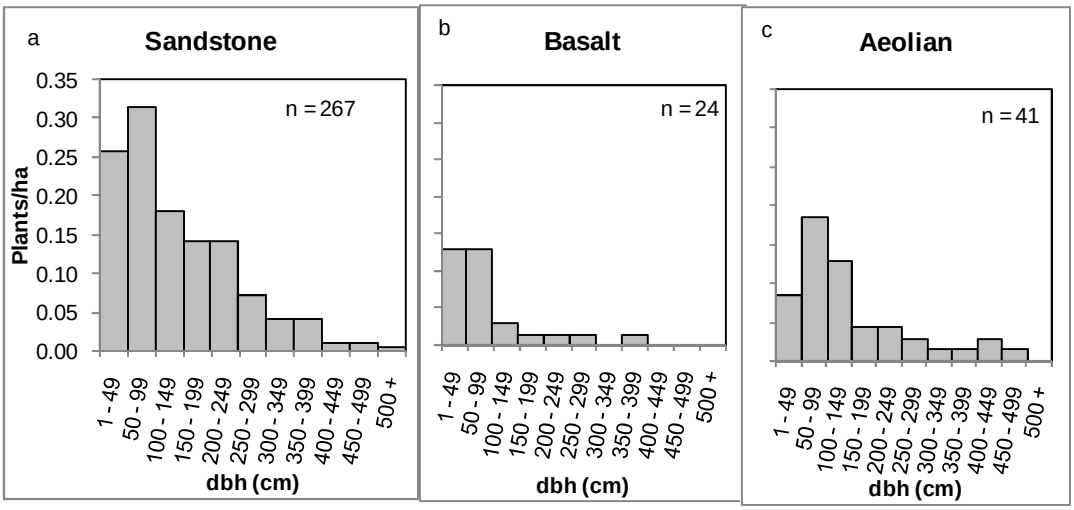

Figure 5. Size-class distribution (50cm dbh intervals) per parent-material type in natural landscapes: Sandstone (a), Basalt (b) and Aeolian (c).

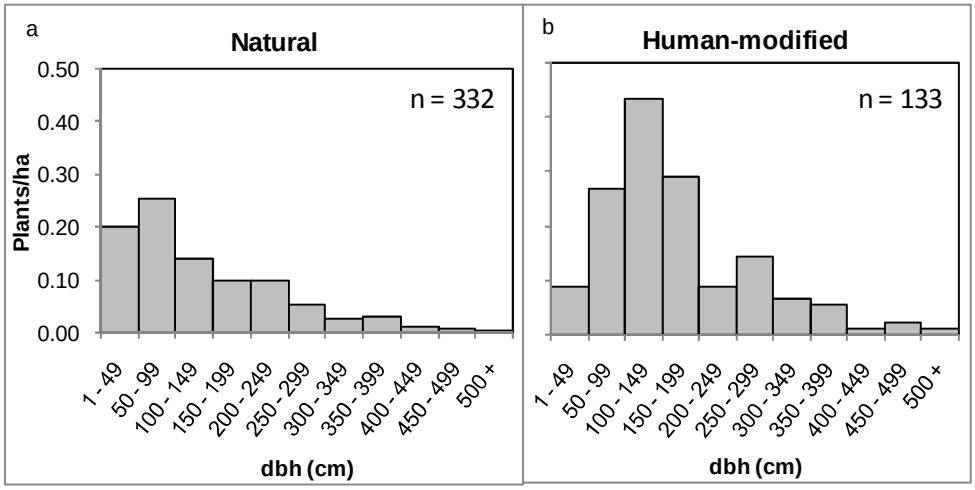

Figure 6. Size-class distribution of baobabs occurring in natural landscapes (a) and human-modified landscapes (b).

3.3 Life stages

Paired t-tests showed that sub-adult and adult densities were similar within all vegetation and soil parent material types (Fig 7, Fig 8). However there tended to be slightly fewer sub-adults than adults in Musina Mopane Bushveld and Limpopo Ridge Bushveld and slightly more sub-adults than adults in Makuleke Sandy Bushveld. Between soils, there tended to be fewer sub-adults than adults in sandstone and aeolian derived soils and more sub-adults than adults in basalt derived soils.

Examination of the densities of sub-adult and adult plants between the different vegetation types showed there were significantly fewer sub-adults in Musina Mopane Bushveld than in Makuleke Sandy Bushveld ($F_{2,69}$=3.4997, p=0.0357) and no difference in

adult densities between all three vegetation types ($F_{2,69}$=1.9071, p=0.1562) (Fig. 7). For parent-materials, there were more sub-adults and adults in sandstone derived soils than in aeolian and basalt derived soils ($F_{2,69}$=3.2443, p=0.0450; $F_{2,69}$=12,916, p<0.001) (Fig.8).

Vegetation types had similar percentages of sub-adults with Makuleke Sandy Bushveld having a slightly higher percentage of sub-adults than Limpopo Ridge Bushveld and Musina Mopane Bushveld (53%, 50% and 46% respectively) (Table 1). Basalt derived soils had a much higher percentage of sub-adults compared to sandstone and aeolian derived soils (75%, 45% and 46%) (Table 1).

SCD slopes were negative for all vegetation types, indicating that there is recruitment in all vegetation types (Table 1). Baobab populations on all soil types also had negative slopes with those on sandstone derived soils having the steepest slope – i.e. best recruitment (Table 1).

The human-modified landscape had significantly fewer sub-adults than adults (t_{22} = -2.3634, p = 0.0274), but the same comparison showed no difference in natural landscapes (t_{22} = 1.1312, p > 0.05) (Fig. 9). Natural landscapes had 49% sub-adults compared to only 24% in human-modified landscapes (Table 1). The SCD slope for the natural landscape was negative, indicating a recruiting population, but flat for human-modified landscapes, suggesting poor recruitment (Table 1).

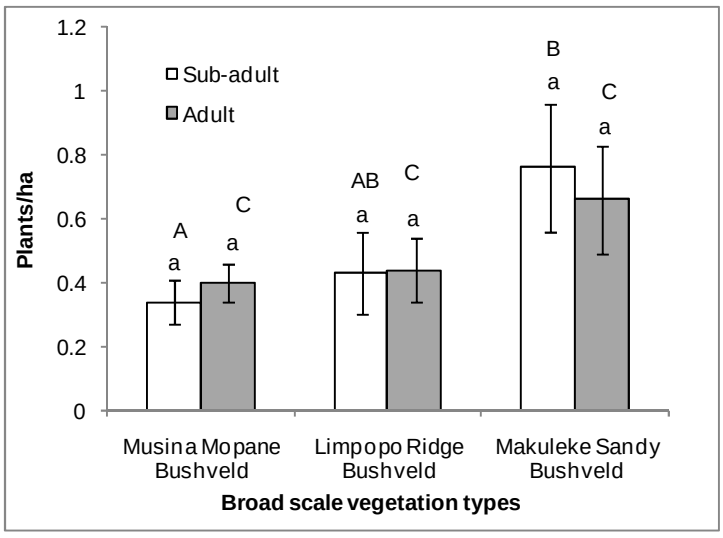

Figure 7. Life stage difference between broad scale vegetation types in natural landscapes. Lower case letters (a) indicate significant differences between life stages within vegetation types. Capital letters indicate significant difference for sub-adult (A,B) and adult (C) plants between vegetation types.

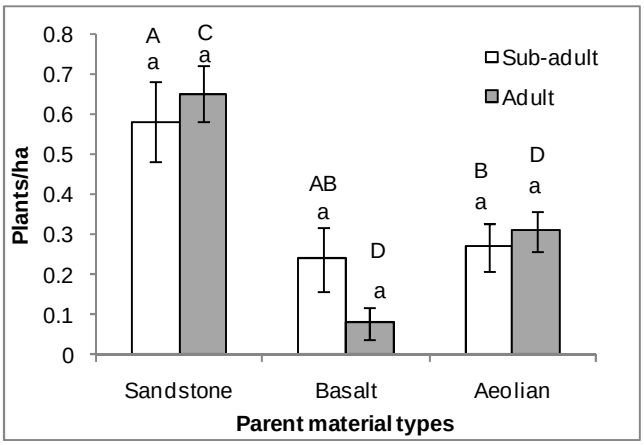

Figure 8. Life stage difference between soil parent material types in natural landscapes. Lower case letters (a) indicate significant differences between life stages within vegetation types. Capital letters indicate significant difference for sub-adult (A,B) and adult (C,D) plants between soil parent material types.

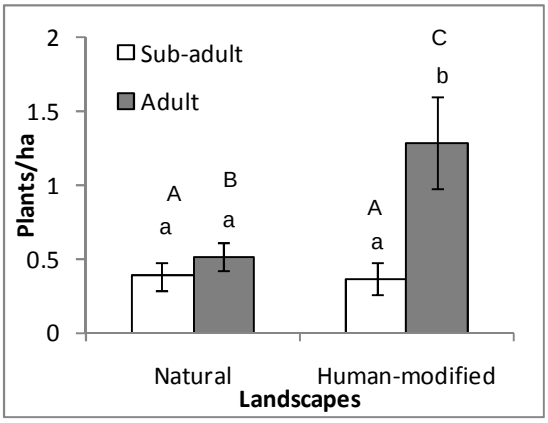

Figure 9 Life stage differences between natural and human-modified landscapes. Lower case letters (a,b) indicate significant differences between life stages within landscapes. Capital letters indicate significant differences for sub-adult (A) and adult (B, C) plants between landscapes.

Table 1. Percentage sub-adults and slope of regression (dbh versus number of individuals) for vegetation types, as well as soil parent-material types within natural landscapes and between natural and human-modified landscapes. * indicates flat slope.

	% Sub-adults	SCD Slope			
		Slope (L)	r^2	t	*p*
Vegetation types					
Musina Mopane Bushveld	46%	-0.20	0.85	-7.21	<0.001
Limpopo Ridge Bushveld	50%	-0.10	0.88	-7.95	<0.001
Makuleke Sandy Bushveld	53%	-0.16	0.73	-4.91	<0.001
Soil parent-material types					
Sandstone	47%	-0.29	0.84	-6.75	<0.001
Basalt	75%	-0.06	0.81	-6.29	<0.001
Aeolian	46%	-0.07	0.56	-3.35	<0.01
Landscapes					
Natural	49%	-0.34	0.84	-6.91	<0.001
Human-modified	24%	-0.09*	0.25	-1.75	= 0.1149

4. Discussion

South of the equator, baobabs occur in the Zambezian eco-climatic zone, where they are associated with a wide variety of vegetation types (Wickens and Lowe, 2008). In the Kruger National Park (KNP), which lies adjacent to the study area, Kelly (2000) and Hofmeyer (2003) found baobabs to be common in sandveld, where *Terminalia sericea* and *Combretum zeyheri* dominate, as well as on the flood plains near the confluence of the Limpopo and Levubu Rivers in vegetation dominated by *C. mopane* and *Acacia tortilis*. This study found baobabs to be associated with similar species as in the KNP.

Baobab densities in the study area differed between vegetation types. Densities of baobabs in Makuleke Sandy Bushveld were higher than in Limpopo Ridge Bushveld and Musina Mopane Bushveld. Similarly, in corresponding vegetation types in the KNP densities of baobabs in Makuleke Sandy Bushveld were higher than in Limpopo Ridge Bushveld (Venter, 1990; Kelly, 2000; Hofmeyer, 2003).

Baobabs are tolerant of a wide variety of soils, including deep sandy soils, shallow lateritic soils and stony soils (Wickens and Lowe, 2008). In our study, there tended to be more baobabs in light sandy soil and light stony soil than in other soil types. However, baobab density was better predicted by parent material than by soil texture (sandy or stony). Baobab populations were significantly denser in soils derived from sandstones than in soils derived from basalts and aeolian deposits. This was also found by Hofmeyer (2003) and Kelly (2000) in the KNP.

The density of baobabs in the natural areas was 0.92 ± 0.02 plants/ha, nine times higher than the density of 0.11 plants/ha reported for the KNP (Kelly, 2000). Lower densities in the KNP may have resulted from high elephant numbers, believed to be responsible for baobab mortality and poor recruitment (Barnes, 1983; Edkins *et al.*, 2007).

The density of trees in human-modified landscapes (villages and fields) (1.65 ± 0.36 plants/ha) was almost twice as high as in natural landscapes (0.90 ± 0.17 plants/ha). This has often been found in other areas of Africa (Duvall, 2007) and has lead to the often asked question: 'did humans settle in areas that already had high baobab numbers or did baobab numbers increase as a result of human activities? Similarly, are humans important dispersers of baobab seeds and responsible for baobab range extension?

Closer examination of the SCD curves for natural and human-modified landscapes reveals that the upper-end (larger classes) of the two SCD curves are similar and that the lower-end (smaller classes) differs. In human-modified areas, the spike in baobab density in the 100-149 cm dbh size-class may have resulted from baobab fruit being brought into villages at a time of *difaqane*/*mfecane* (wondering hordes) when people may have needed to rely heavily on natural resources as a result of insecurity and military stress (Huffman, 2007). This together with a wet period and warmer conditions around 1800 (Huffman, 2007) may be a reason for high numbers in this size class. Since then, increasing livestock numbers, expansion of fields and villages and a dryer climate may have resulted in poor recruitment, as is reflected in the smallest size-class (0 – 49cm dbh). The significantly lower sub-adult population density relative to adult density, and flat SCD slopes also indicate that recent changes in land management practises in human-modified landscapes is hampering recruitment. The lack of smaller size-classes also indicates how baobabs have lost importance for local people in recent years, as there is no planting or active protection of baobab seedlings from livestock damage, as is seen in West Africa (Duvall, 2007).

5. Conclusion

In natural landscapes, baobab densities and not size-class distributions, differed significantly between vegetation types and soil types. The densities of trees in human-modified landscapes were almost twice as high as in natural landscapes, suggesting a higher rainfall regime and/or a higher use of baobab fruit, in the past. However bell-shaped SCDs, low sub-adult density and flat SCD slopes indicate that current management practices are hampering recruitment. The reasons for this should be investigated so that appropriate management actions can be taken to maintain this population into the future.

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Chapter 4

Published paper

Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa

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Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa

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ABSTRACT

Baobab fruit are harvested and used throughout Africa as an important source of food and are sold to generate income. Commercial use is increasing rapidly as derivatives of the fruit such as baobab seed oil and fruit pulp are being exported to Europe and North America. The cash derived from the sale of fruit support thousands of rural people. This study examines baobab fruit yields in an area being harvested for commercial use. It represents baobab populations and harvesting scenarios typically found in Southern Africa and is the first study in Africa to combine demographic and production data in determining baobab fruit yields.

Fruit production was examined across five land-use types (nature reserves, rocky outcrops, plains, fields and villages) and over three consecutive years. Factors assessed included differences in life-stage, tree size, land-use type, inter-annual variation and quantifiable fruit predation.

Results showed that adult trees produced 8 times more fruit than sub-adult trees. Fruit production fluctuated between size-classes and exhibited weak linear and logarithmic trends between fruit production and dbh and crown volume, respectively. There was high variation between trees with 41% of adult trees consistently producing <5 fruit per year, which we classed as 'poor-producers'. Different land uses showed no significant differences in fruit production per tree, but where baboons were present, in nature reserves and rocky outcrops, predation of immature fruit resulted in up to 85% fruit loss. Villages and fields had the highest tree density and yielded the most fruit/ha. Inter-annual variation was significant with a two and a half fold difference between the highest and lowest year.

The results of this study are important for economic planning and management and are key to determining sustainable harvesting levels of baobab fruit in Southern Africa.

1. Introduction

Baobabs (*Adansonia digitata* L. (Malvaceae)) are valued in Africa for food, fibre and medicine. Where baobab products are sold in informal markets, they form an important source of income for thousands of rural people (Sidibe and Williams, 2002). Recently derivatives of the fruit, such as baobab seed oil and baobab fruit pulp, have been exported to countries outside Africa, mainly Europe, Canada and the USA. As baobab extracts become more popular, it is predicted that the demand for the resource will grow (Sidibe and Williams, 2002). Such commercial use of the fruit provides an income to many thousands of people throughout Africa. In Zimbabwe, for instance, the sale of baobab fruit has increased the income of rural people by 250% (Gruenwald and Galizia, 2005). It is therefore important that the resource is managed sustainably. One of the first steps in achieving this goal is to gain a thorough understanding of the biology and ecology of baobabs, for which there is surprisingly little information.

Sustainable utilization of non-timber forest products (NTFPs) is essential for the conservation of the plants and for the livelihoods of the rural people who depend on them (Ticktin, 2004). For most NTFPs there is too little information to make informed decisions about sustainable harvesting and management (Chamberlain, 2003; Lawes et al., 2004) and this also applies to baobab products. Many baobab studies have focused on food value, socioeconomic importance, ethnobotanical knowledge, taxonomy, morphology and genetic aspects (Dovie, 2003; Wickens and Lowe, 2008; Assogbadjo et al., 2009; De Caluwe et al., 2009; Tsy et al., 2009). However, in order to determine NTFP yields, reliable data is necessary on population demographics and plant production levels associated with plant size, site characteristics, predation and inter-annual variation (Goldwin, 1992; Peters, 1996; Tilman, 1997; Fenner and Thompson, 2005).

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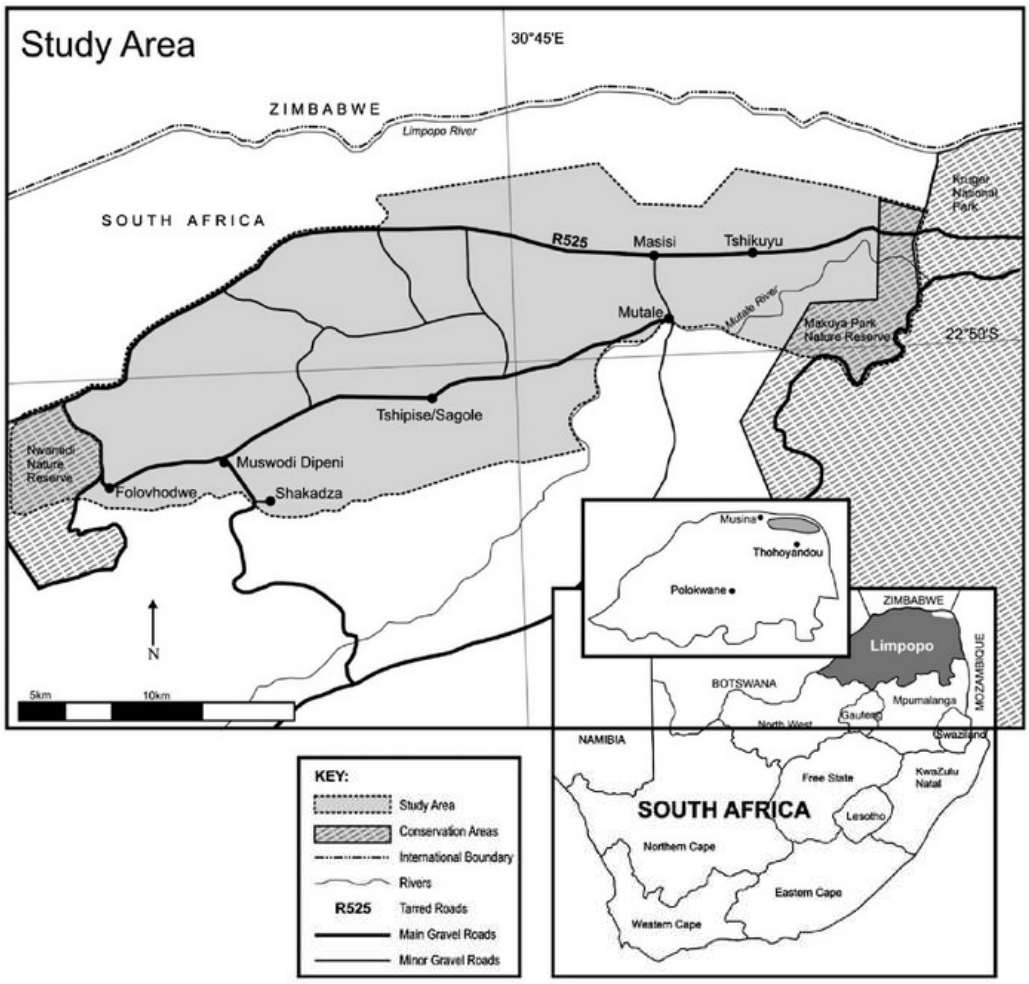

Fig. 1. Map indicating location of study area in Limpopo Province, South Africa.

Whilst baobab demographic studies have been done in various parts of Africa (Kelly, 2000; Hofmeyer, 2001; Dhillion and Gustad, 2004; Assogbadjo et al., 2006; Chirwa et al., 2006; Edkins et al., 2007; Venter and Witkowski, 2010), few have assessed the amount of fruit produced by trees and the factors that influence fruit production (Dhillion and Gustad, 2004; Assogbadjo et al., 2005; Cuni Sanchez et al., 2009). Hence, the aim of this study was to determine differences in fruit production between land-use types, between tree life-stages, size-classes and between successive years.

Commercial use of baobab fruit began in the northern part of South Africa in 2005. Fruit is collected from trees in fields, villages and surrounding communal land by local people, mainly otherwise unemployed women. They are processed *in situ* and sold to a locally-based company that makes oil from the seeds and packages the fruit pulp. The resulting products are sold to the markets as cosmetic and food ingredients. Similar arrangements occur throughout sub-Saharan Africa (Gruenwald and Galizia, 2005). Income from the sale of baobab fruit in northern South Africa goes to over 1500 people for whom this forms part of their livelihood strategy (Venter, unpublished data). These commercial fruit harvesting activities prompted this study on fruit production in this area.

Baobab fruit production was studied over three seasons and across five land-use types within conservation areas and communal land. It was predicted that there would be high fruit losses in land-use types where baboons were present, such as nature reserves and rocky outcrops. In addition trees in villages and fields would be more productive than trees in other land-use types due to higher soil fertility and sparser ground cover reducing competition for limited ground water. Fruit production was expected to vary with tree size and that there would be high inter-annual variation depending on rainfall with higher fruit production in high than in low rainfall years. The paper also evaluates the methods used to determine baobab fruit yields and recommends further studies to improve the sustainable management of baobab resources.

The findings are discussed in relation to a fascinating study by Assogbadjo et al. (2008, 2009) on 'male' and 'female' characteristics of baobab trees. Baobabs have hermaphroditic flowers (both male and female parts in the same flower) (Baum, 1995a), yet local people throughout Africa distinguish between 'male' and 'female' trees. Assogbadjo et al. (2008) describe 'male' baobabs as producing very few fruit and 'female' baobabs as producing many fruit. In this study these trees are called 'poor-producers' and 'producers'. The

paper provides further information on the extent of this tendency and its impacts on fruit yield predictions.

Given that seed oil is being extracted from many other African tree species, the study provides a template for similar studies in other species.

2. Materials and methods

2.1. Study area

The research was conducted in the northern part of Limpopo Province (around 22°19′S and 30°28′E), South Africa. The area is commonly known as northern Venda and is about 1250 km^2 in size. Two provincially-managed nature reserves formed part of the study area; Nwanedi Nature Reserve lies in the west, and Makuya Nature Reserve in the east (Fig. 1). This area represents about 10% of the distribution of baobabs in South Africa (Palgrave, 1983).

The study area falls within the Zambezian regional centre of endemism which includes Angola, Namibia, Botswana, Zambia, Zimbabwe, Mozambique and South Africa. Baobabs are common in *Colophospermum mopane* (mopane) woodland within this region (Wickens and Lowe, 2008). Mucina and Rutherford (2006) describe the area broadly as the Savanna Biome with the following specific vegetation types: Musina Mopane Bushveld, Limpopo Ridge Bushveld and Makulele Sandy Bushveld which are dominated by *Colophospermum mopane* (mopane), *Terminalia sericea* (silver terminalia), *Grewia flava* (brandybush) and *Combretum apiculatum* (red bushwillow). Vegetation in general is low sparse woodland with an average tree height of 4–5 m and a tree cover of 20% with emergent baobabs (Butt et al., 1994). Bush fires are not common due to low grass and herb biomass, and elephants are infrequent visitors.

The average altitude of the region is 400 m above mean sea level and has a gently undulating topography underlain by sandstones of the Karoo Supergroup and the Clarens and Letaba Formations (Brandl, 1981; Mucina and Rutherford, 2006). Soils are generally deep sands and shallow sandy lithosols (Mucina and Rutherford, 2006).

Northern Venda is semi-arid with a rainfall averaging between 334 and 423 mm and a high coefficient of variation of 35–40% (Schulze, 1997). Summers (October–March) are characteristically hot and winters (April–September) are mild. Frost seldom occurs (Mucina and Rutherford, 2006).

Poverty and low employment are endemic to Venda so subsistence agriculture is important. The ratio of men to women is 1:4 with a 0.78–2.38% level of formal employment (Statistics-S.A., 2001). Wooded plains, interspersed with sandstone outcrops are used mainly for grazing cattle, goats and donkeys. There is open access to these natural resources with minimal control from traditional institutional structures and government.

2.2. Study species

Adansonia digitata is one of the eight species of baobab in the genus *Adansonia* L. (Malvaceae, subfamily Bombacoideae) and the only one which naturally occurs on mainland Africa. It is present throughout most of Africa south of the Sahara (Baum, 1995b). In South Africa the population is limited to the Limpopo River valley, with the exception of a few isolated trees found further south (Wickens and Lowe, 2008).

Phylogeographic research show that baobabs originated in West Africa and spread by human-assisted dispersal to the rest of Africa. Three distinct groups of baobabs are found, two in West Africa and the third in Southern and Eastern Africa. Baobabs in Southern and Eastern Africa can be regarded as one phylogeographic population due to low genetic variation within this group (Tsy et al., 2009).

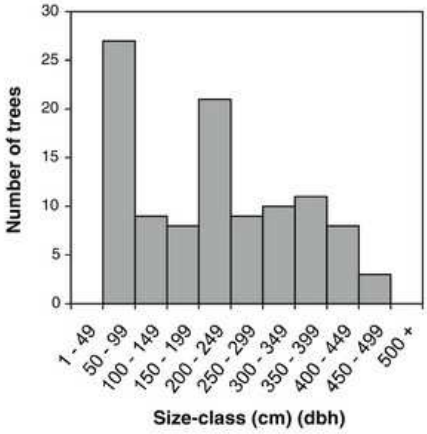

Fig. 2. Number of sampled trees per size-class.

Baobabs are deciduous, bearing leaves and flowers in the wet season (Wickens, 1982; Baum, 1995a). In well watered environments, such as gardens, trees grown from seed can start to flower from 16 to 22 years of age (Pardy, 1953; Wickens, 1982). However in natural semi-arid environments, it is expected that trees may only start flowering at 125 years of age (Swanepoel, 1993). Flowering usually lasts 4–6 weeks with a few flowers opening each night (Baum, 1995a). The period between flowering and fruit ripening is 5–6 months (Sidibe and Williams, 2002). Developing flowers and fruit are a rich source of food, and are eaten and parasitized by a variety of animals including insects, birds and mammals (Wickens, 1982; Hulme, 2001; Pochron, 2005). Baobabs are known to be extremely long-lived trees and despite the softness of their wood can live to at least 1200 years (Von Breitenbach and Von Breitenbach, 1985; Patrut et al., 2007).

2.3. Sampling and measurement

Field work was done over three summer seasons, starting in October 2006 and ending in March 2009. Measurements were taken in five land-use types: (1) nature reserves; (2) plains; (3) rocky outcrops; (4) fields and (5) villages. Except for nature reserves, all of these represent different categories of communally-managed land. Trees were selected to include a wide range of stem diameters in each land-use type (Fig. 2). In total 106 trees were chosen, 34 in nature reserves and 18 in each of the other land-use types. Each tree was considered a sample. Rain gauges were erected at three village homesteads across the study area and local people were employed to record daily rainfall.

For each tree the following five single measurements were taken: geographic position (latitude and longitude); tree girth (measured with a glass-fibre measuring tape at 1.3 m above the ground) and converted into stem diameter at breast height (dbh); tree height (estimated to the closest 2 m, i.e. 2, 4, 6); crown width (measured to the closest meter under the tree as two perpendicular lines, i.e. A1 north–south and A2 east–west orientation); crown height (CH) which was the vertical length of the crown from the lower branches to the top of the tree. Crown volume (CVOL) was calculated using the formula in Snook et al. (2005). First the crown projection area (CPA) was calculated using the equation for an ellipse: $CPA = [(A1/2) \times (A2/2)]\pi$, then crown volume (CVOL) was calculated by $CVOL = CPA \times CH \times 0.5$.

Trees were visited every 1–2 months during the first two summer seasons (October 2006–May 2008). During the third summer

season only one assessment was done, in March 2009. Three categories of fruit were counted at each visit: (1) fruit on the tree, (2) immature wind-blown fruit on the ground (this does not include mature fruit that drop off the tree at the end of the season) and (3) immature predated fruit (eaten by baboons off the tree). Baboons ate newly formed soft fruit which appear on trees a few weeks after first flowering. Baobab fruit take 5–6 months to mature (Sidibe and Williams, 2002), thus these fruit do not have viable seed and predation, this early in the season, does not contribute to seed dispersal. Baboons ate fruit by taking one or two bites and then discarding the remains on the ground below the tree. In order to quantify predated fruit accurately, the stalk of each eaten fruit was counted and discarded so that it would not be counted again at the next visit.

Data analysis used two categories of fruit, total and mature fruit. Total fruit was the sum of mature fruit (counted at the end of the season) plus immature windblown fruit and immature predated fruit lost during the growing season. Total fruit represents the capacity of trees to produce fruit. All sampled trees were used to compare total fruit production between life-stages, tree sizes and land-use types. The second category of fruit was mature fruit, which excluded immature wind-blown and immature eaten fruit. Fruit was regarded as mature once the shell had hardened and the fruit pulp became powdery which happens at the end of the wet season. Thus fruit counted in March/April represented mature fruit. This distinction is important for recruitment and socio-economic studies.

For analysis of fruit size, only trees that had mature fruit were used. Trees in nature reserves, where fruit predation was particularly high, were not used in fruit size analysis. Matured fruit was divided into three size categories, small (±10 cm × 5 cm), medium (±15 cm × 8 cm) and large (±20 cm × 10 cm). Fruit size was based on fruit length (top to bottom) and fruit diameter (measured midway between top and bottom).

2.4. Data analysis

Inter-annual variability in fruit production (2006–2009) was analysed using Friedman ANOVA (Q) and the methods described in Herrera (1998) to determine population level variability (CVp), within plant variability (mean CVi) and among plant synchrony (W; Kendall coefficient of concordance). When population level variability is equal to within plant variability then there is high between plant synchrony (Herrera, 1998). Size-class distributions for fruit production were constructed for each year to allow for visual comparisons and to test for differences using Kolmogorov–Smirnov tests. The Cochran Q-test was used to compare proportion of fruiting and non-fruiting trees between years. Friedman ANOVA (Q) with Kendall coefficient of concordance (W) was used to analyse the differences in the proportion and number of different sized mature fruit per tree produced between and within each year, respectively.

t-Tests were used to assess the contribution of life-stage to differences in total fruit production. Life-stage was arbitrarily categorized as sub-adult (<100 cm dbh) and adult (≥100 cm dbh). The contribution each life-stage made to fruit production was given as a percentage of total production. A Yates corrected χ^2 2 × 2 contingency table was used to analyse the proportions of fruit-bearing and non-fruit-bearing trees between life-stages.

To determine if sub-adult trees tended to produce smaller fruit than adult trees, three separate t-tests were done to compare the proportions of small, medium and large-sized matured fruit between life-stages.

The proportion of sub-adult and adult trees falling into each total fruit production class (0–4; 5–24, 25–49, 50–99, 100–199, 200–299, 300–399, 400–499, ≥500 fruit/tree) was determined. Adult trees that produced an average of <5 total fruit/year over three years were termed 'poor-producers', the rest were called 'producers'. t-Tests were done to determine if there were significant differences in total fruit production and stem diameter (dbh) between the two categories. A χ^2 2 × 5 contingency table was used to determine if there were differences in the number of trees of each category within each land-use type. Friedman ANOVA with Kendall coefficient of concordance (W) tested inter-annual variation in fruit production for 'poor-producers'.

Trees were divided into 50 cm dbh size classes and the mean number of fruit per tree per size-class was displayed graphically. To determine whether a senescent category should be defined, a t-test compared fruit production between the largest and second largest size-class. Regression analyses were performed to test the following: the relationship between tree dbh, crown-volume and crown-area; total fruit production as a function of tree size (dbh); and the influence of tree size (dbh) on size of fruit.

Both total fruit production and mature fruit production were compared between five land-use types using ANOVA followed by Fisher's Least Significant Difference tests (LSD, $p < 0.05$). The proportions of small, medium and large-sized fruit were determined for each communal land-use type. Friedman ANOVA (Q) with Kendall coefficient of concordance (W) tested for inter-annual variation in total fruit production within each land-use type.

The proportion of predated fruit from trees that produced fruit in each land-use type was compared using ANOVA followed by Fisher's LSD ($p < 0.05$). Using a χ^2 2 × 2 contingency table with Yates correction, the number of trees which did and which did not have predated fruit was compared between land-use types where baboons were common (nature reserves and rocky outcrops) against those where baboons were scarce (plains, fields and villages). Regression analysis compared the proportion of predated fruit against tree size (dbh). The inter-annual differences in the proportion of fruit predated per year was analysed using Friedman ANOVA (Q) with Kendall coefficient of concordance (W). The Cochran Q-test compared the number of trees which did and did not have predated fruit over three years.

A population demographic study was done by Venter and Witkowski (2010) where density of baobabs in different communal land-use types (excluding nature reserves) was determined for the same study area. Using these population data, adult stems/ha were multiplied by adult mature fruit/tree and fruit size figures to determine total fruit yields for the area and for each communal land-use type.

3. Results

3.1. Annual variability in fruit production

The number of fruit produced per year differed significantly between sampling years ($Q_{2,106} = 13.8304$, $p = 0.0009$). Fewer fruit were produced in 2007/2008 than in the preceding (2006/2007) and subsequent year (2008/2009) (Table 1). Inter-annual variability was more strongly determined by within plant variability rather than by between plant synchrony (CVp = 44.7, mean CVi = 104.8, W = 0.1320). Fruit production per dbh size class showed high variability between years (Fig. 3b–d) and signifi-

Table 1
Annual variability in fruit production over three years and annual rainfall (July – June).

Annual variability	Rainfall (mm)	Fruit/tree (mean ± SE)
Year 2006/2007	275	81.7 ± 18.1[a]
Year 2007/2008	484	29.7 ± 6.6[b]
Year 2008/2009	334	68.7 ± 15.3[a]

Different superscript letters indicate significant differences between years ($p < 0.001$).

Table 2
Differences between sub-adult and adult life-stages.

Life stages	Proportion of trees producing fruit	Fruit/tree (mean ± SE)	Proportion of fruit per tree (mean ± SE)		
			Small	Medium	Large
Sub adult	0.44[a]	9.9 ± 4.7[a]	0.38 ± 0.01[a]	0.39 ± 0.10[a]	0.23 ± 0.07[a]
Adult	0.81[b]	77.1 ± 13.8[b]	0.32 ± 0.03[a]	0.44 ± 0.03[a]	0.24 ± 0.03[a]

Different superscript letters indicate significant differences between life stages ($p < 0.05$).

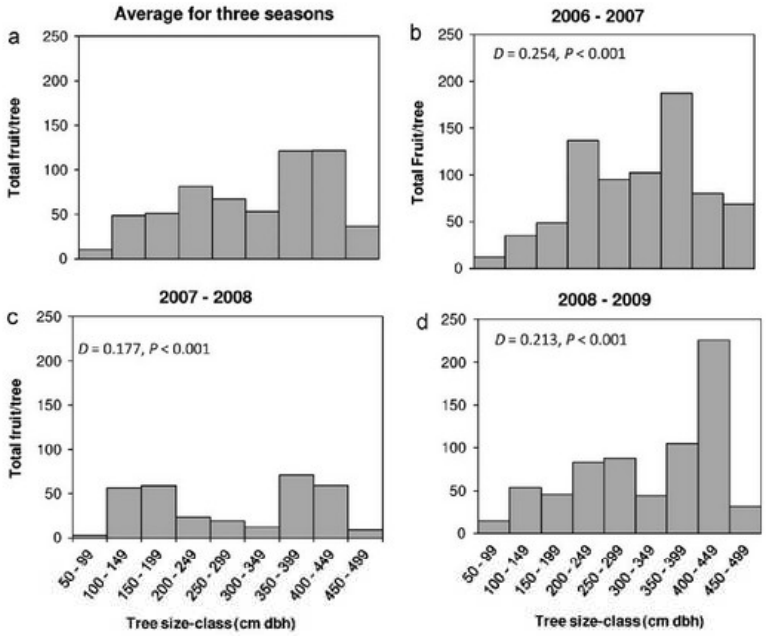

Fig. 3. Mean fruit production per tree size-class ($n = 106$ trees) per year over three seasons (a), and for each season: 2006–2007 (b), 2007–2008 (c), 2008–2009 (d). Kolmogorov Smironov test (D) results for differences in size-class distributions between are also shown.

cant Kolmogorov–Smirnov results. The proportion of trees that produced fruit each year did not differ significantly ($Q = 3.9200$, $p = 0.1409$). Fruit sizes fluctuated significantly between and within years (Fig. 4).

3.2. Comparisons of fruit production between and within life stages

Adult trees produced significantly more fruit per tree than sub-adult trees ($t_{104} = 2.799$, $p = 0.006$) and a significantly greater proportion of adult trees produced fruit than sub-adult trees ($\chi^2_{Yates} = 11.52$, $p < 0.001$) (Table 2). In total, adult trees produced 8 times more fruit than sub-adult trees. In communal land 51% of all trees produced matured fruit. For these the proportion of small, medium and large-sized matured fruit did not differ between life-stages ($t_{35} = -0.9281$, $p = 0.3597$; $t_{35} = 0.4841$, $p = 0.6313$; $t_{35} = 0.5522$, $p = 0.5843$) (Table 2).

The majority (74%) of sub-adults produced less than 5 fruit per year in contrast with 41% of adult trees (Fig. 5). These trees, in the adult life-stage are categorized as poor producers in the next section. The majority of adult trees (59%) produced less than 25 fruit per tree per year and 36% of adult trees produced between 50 and 299 fruit and only 5% produced ≥300 fruit per year (Fig. 5).

Fruit production in adult trees was significantly higher in 'producers' than 'poor-producers' ($t_{77} = -5.2740$, $p < 0.001$), with 'producers' contributing to over 99% of fruit production (Table 3). There was no significant difference in stem diameters ($t_{77} = 1.4961$, $p = 0.1387$) between 'producers' and 'poor-producers' (Table 3). There was also no significant difference in the numbers of 'producers' and 'poor-producers' in each land-use type ($\chi^2_4 = 3.868$, $p = 0.5758$). Fig. 6a shows that 'poor-producing' trees were present in all tree size-classes. 'Poor producing' trees do not produce fruit every year and 47% of these do not produce fruit at all (Fig. 6b). No significant inter-annual variation in fruit production was found

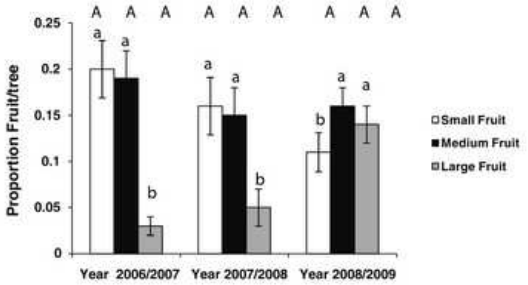

Fig. 4. Proportions of different sized fruit per tree between and within seasons. Capital letters (A,B) show significant differences between seasons and lower case letters (a,b) within seasons ($p < 0.05$). These fruit numbers exclude eaten and wind-fallen fruit which did not reach final mature fruit size.

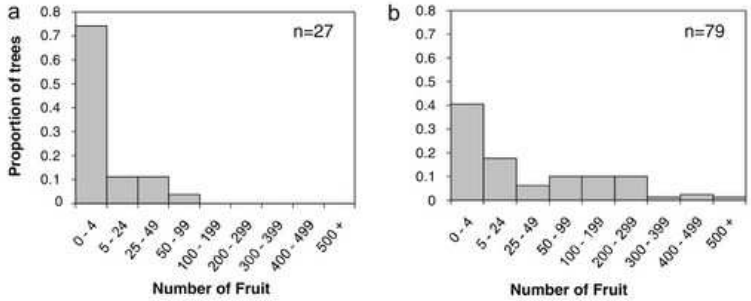

Fig. 5. Proportions of sub-adult (a) and adult (b) trees per fruit number class.

Table 3
Differences between adult 'producer' and 'poor-producer' baobab trees ($n = 79$).

Producer & poor producer	Trees in population (%)	Fruit produced (%)	Stem diameter (cm) (dbh)
Poor producers	41%	0.3%	255 ± 18[a]
Producers	59%	99.7%	293 ± 14[a]

The same superscript letter indicates no significant differences ($p < 0.05$).

in poor-producers ($Q_{(2,32)} = 4.5657$, $p = 0.1035$, $W = 0.0708$) which means that these trees consistently produce few fruit.

3.3. Size-class trends

There were weak logarithmic trends between crown volume and fruit production ($p < 0.001$, $R^2 = 0.1213$) and crown area and fruit production ($p < 0.001$, $R^2 = 0.1020$) and strong linear trends between crown volume and dbh ($p < 0.001$, $R^2 = 0.5373$) and crown area and dbh ($p < 0.001$, $R^2 = 0.5904$). Total fruit production fluctuated between size-classes (Fig. 3a), with a weak positive linear trend between fruit production and dbh ($p = 0.0043$, $R^2 = 0.0756$). In the largest size-class (450–500 cm dbh) fruit production dropped off, but not enough to define a senescent category ($t_9 = 0.7210$, $p = 0.4892$).

Regression analyses of the proportion of different sized fruit showed a weak negative trend between small-sized fruit and dbh ($p = 0.0153$, $R^2 = 0.1566$). Weak positive trends but no significant relationships were found for medium or large-sized fruit and dbh ($p = 0.2490$, $R^2 = 0.0378$; $p = 0.1336$, $R^2 = 0.0631$).

3.4. Comparisons of fruit production between land-uses

There was no significant difference in total fruit production between land-use types ($F_{4,101} = 1.2078$, $p = 0.3122$) (Fig. 7a). However due to fruit predation (see next section) significant differences were found in final mature fruit numbers between land-use types ($F_{4,101} = 8.6286$, $p < 0.0001$) (Fig. 7b). A greater proportion of medium-sized fruit was produced in all land-use types except villages, where an equal proportion of small-sized and medium-sized fruit were produced (Fig. 7c). Fruit production also differed significantly between the three years within all land-use types except for rocky outcrops (rocky outcrops: $Q_{2,18} = 1.3778$, $p = 0.5021$, $W = 0.0382$; plains: $Q_{2,18} = 13.4737$, $p = 0.0012$, $W = 0.3742$; fields: $Q_{2,18} = 10.8000$, $p = 0.0045$, $W = 0.3000$; villages: $Q_{2,18} = 10.3044$, $p = 0.0057$, $W = 0.2862$; nature reserves: $Q_{2,34} = 14.1123$, $p = 0.0009$, $W = 0.2075$).

3.5. Predation

The proportion of fruit predated from trees that produced fruit in rocky outcrops and nature reserves was much higher than from those found in plains, fields and villages ($F_{4,48} = 86.951$, $p < 0.001$). In the latter three land-use types, predation was negligible (Fig. 8a). Fewer trees with predated fruit where found in areas where baboons were seldom found (plains, fields and villages) ($\chi^2_{\text{Yates}} = 11.52$, $p < 0.001$) (Fig. 8b). Regression analysis showed no relationship between tree size and proportion of fruit predated ($R^2 = 0.0133$, $p = 0.4060$). There was also no significant difference in the proportion of fruit predated between years ($Q_{2,40} = 4.0274$, $p = 0.1335$, $W = 0.0503$) nor in the number of trees that had predated fruit ($Q = 2.666$, $p = 0.2636$).

3.6. Estimated fruit yields

Venter and Witkowski (2010) determined that there were 0.90 ± 0.18 stems/ha of adult baobab trees in the population as a whole, with 0.47 ± 0.31 occurring in plains, 0.56 ± 0.31 in rocky

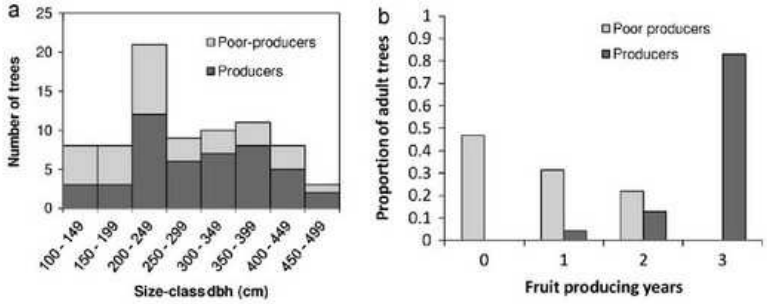

Fig. 6. Number of 'producing' and 'poor-producing' trees in adult size-classes (a) and the proportion of 'producer' and 'poor-producer' trees producing fruit by number of years over the 3 year study period (b).

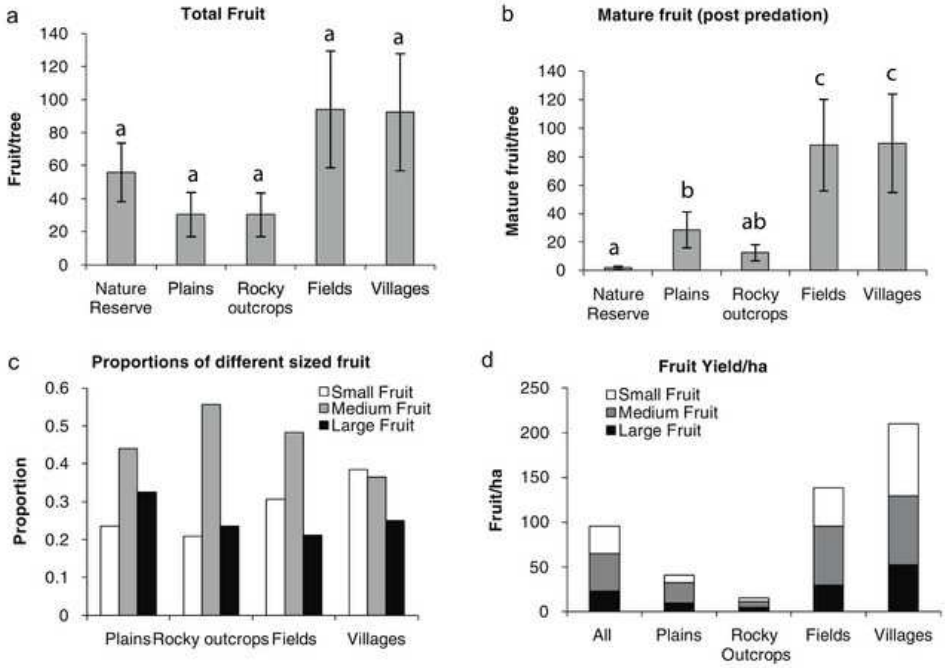

Fig. 7. Land-use type differences in mean total fruit (a), mean mature (post-predation) fruit (b), proportions of small, medium and large-sized fruit in different communal land-use types (c) and mature fruit yields per hectare for all communal land-use types (d). Fruit yields were calculated using stem density data from Venter and Witkowski (2010). Lower-case letters (a–c) indicate significant differences ($p < 0.05$).

outcrops, 0.87 ± 0.3 in fields and 1.7 ± 0.31 in villages. The combination of high tree densities and high fruit yields showed villages and fields to have produced the highest number of fruit per hectare and plains and rocky outcrops the least (Fig. 7d). The population as a whole produced 96 fruit/ha on communal land-use types with similar proportions of small, medium and large sized fruit.

4. Discussion

The estimation of fruit yield is important for economic planning and management and is key to determining sustainable levels of resource extraction, particularly for fruit which have a high socio-economic value such as baobabs (Chamberlain, 2003; Cunningham and Shackleton, 2004; Ticktin, 2004; Shackleton et al., 2005). Fruit inventories can be time consuming and costly therefore knowing what factors have an influence on fruit production can help make them more efficient and accurate.

Stem diameter and crown volume are often used as predictors of fruit production. However these are generally only accurate for species with small fruit and not for species with large fruit, such as baobabs (Chapman et al., 1992; Botelle et al., 2002; Shackleton et al., 2002; Killmann et al., 2003). Killmann et al. (2003) tested methods for assessing baobab fruit production in Kenya and suggested that stem diameter and crown size cannot be used as indicators of fruit production because fruit production was extremely variable. They suggested that visual counts of fruit on primary or randomly selected branches would be the most accurate and efficient method.

Similarly our study showed that stem diameter (dbh), crown volume and crown area were too poorly related to fruit production (low R^2 values) to allow the use of these variables as predictors of fruit production. However, stem diameters can reliably be used to distinguish between sub-adult and adult trees. Our study showed that sub-adults produced very few fruit, thus excluding

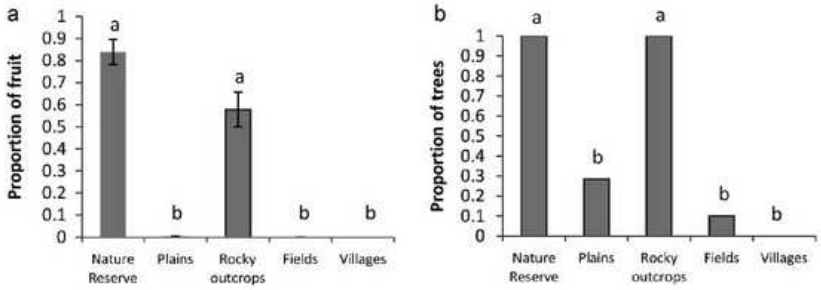

Fig. 8. Proportion of fruit predated per land-use type (a) and proportion of trees which had fruit predated per land-use type (b). Lower-case letters (a,b) indicate significant differences ($p < 0.001$).

trees <100 cm dbh (sub-adults) would make fruit inventories more efficient.

Fruit production figures from other parts of Africa are limited or not widely published. Ibiyemi et al. (1988) quoted an unsubstantiated figure of 250 fruit per mature plant. In contrast, Swanepoel (1993) reported that, over a four year period, baobabs in the Mana Pools area of the Zambezi River valley did not produce any mature fruit. He attributed this to the trees not having enough reserves to produce fruit after leaf flush and flowering, and that bark stripping by elephants may also have reduced the capacity of trees to produce fruit. No mention was made of baboon predation which could have been the main reason for poor fruit production. Assogbadjo et al. (2005) reported that mean fruit production in Benin varied between 57.1 and 157.4 fruit per tree in different climatic zones. Fruit production in communal land in South Africa of 77.1 ± 13.9 (SE) thus falls within the levels found in Benin.

Site characteristics can influence fruit production (Peters, 1996). Assogbadjo et al. (2005) found that variability in site conditions across three climatic zones in Benin significantly influenced baobab fruit productivity. Our study found that total fruit production (when including predated fruit) did not differ between land-use types, but tended to be higher in human-modified landscapes (fields and villages) and lower in natural landscapes (nature reserves, plains and rocky outcrops). Sparse ground cover resulting in reduced inter-plant competition, dripping taps (pers. obs.) which increases moisture availability–a limited resource in this arid environment, may have been responsible for the slight increase in fruit production in villages and fields.

Predation of immature baobab fruit by baboons, although not quantified, has been observed elsewhere in Africa (Wickens, 1982; Pochron, 2005; Kunz and Linsenmair, 2007; Watson, 2007). In our study fruit production was reduced by between 58% and 85% in areas where baboons were found, in contrast to 0% and 1% in areas where baboons were scarce. As baboons eat fruit that do not contain mature seed they contribute to seed destruction rather than dispersal. This shows the dramatic effect baboon predation can have on final mature fruit yield and therefore the presence of baboons needs to be taken into account when assessing areas for fruit harvesting and recruitment. Furthermore baobab populations are threatened by elephant populations (Edkins et al., 2007) in nature reserves and together with the prevalence of baboons, populations are likely to decline further in the long-term and in the end will predominate in refugia where elephant densities are low.

Baobab trees produce a wide variety of different fruit sizes (Gebauer et al., 2002; Sidibe and Williams, 2002; Assogbadjo et al., 2005). In Benin, differences in fruit size and shape are so pronounced that people use these, in addition to other morphological characteristics, to distinguish between types of baobab (Assogbadjo et al., 2008). Studies on genetic variation could not find a genetic explanation for the production of different sized fruit (length) (Assogbadjo et al., 2009).

We found that adult trees tended to produce more medium-sized (44%) than small (32%) and large-sized fruit (24%). The larger the fruit the more seed and fruit-pulp they have (Venter, unpublished data), thus by including fruit-size differences in fruit inventories, more accurate predictions of total seed, seed oil and fruit-pulp can be made.

High inter-annual variability makes predicting fruit production and assessing the economic and ecological sustainability of commercial fruit harvesting very difficult (Botelle et al., 2002; Shackleton, 2002). Our study indeed showed high inter-annual variation. Fruit production varied from as much as 81.7 ± 18.1 fruit per tree in 2006/2007 to as little as 29.7 ± 6.6 fruit per tree in 2007/2008, a two-and-a-half-fold difference between the highest and lowest year. Smaller trees showed less variation than larger trees, as has been found for other species (Snook et al., 2005). The overall number of fruit-bearing trees did not differ between the years yet trees exhibited high within tree variability and weak between tree synchrony. Rainfall figures did not correspond to in-season fruit production. The year (2007/2008) that produced the fewest fruit had the highest rainfall. Similarly Shackleton (2002) found that fruit production in marula (*Sclerocarya birrea*), another highly valued fruit species, could not be explained by rainfall during the current growing season. He suggested that the rainfall in the preceding season might have had a greater influence on fruit production. To understand the factors that influence fruit production between years would require a much longer and more expansive study.

We categorized adult trees that produced <5 fruit a year as 'poor-producers', the rest of the adult trees we called 'producers'. Assogbadjo et al. (2008, 2009) described 'male' trees as those that produce few fruit and 'female' trees as those that produce many fruit. This could be equated to what local people in the Venda study area refer to as male (poor-producers) and female trees (producers) and they say that poor-producers are consistently so over many years (Venter, unpublished data). Tree size did not have an influence on whether trees were 'producers' or 'poor-producers' and neither did land-use type. Although we do not know what is driving this pattern, it appears that environmental conditions do not play a role because 'poor-producers' and 'producers' were often observed next to each other, presumably sharing the same soil and water conditions. Assogbadjo et al. (2009) did not find genetic difference between trees with these traits and suggested that the poor fruit production in 'male' trees may be due to self-incompatibility. Physical characteristics that could distinguish between 'poor-producers' and 'producers' where not observed by us and until these trees can be easily identified, large sample sizes would be required to get accurate predictions of population level fruit production. Further data is required to assess flowering and fruit-set patterns and to describe the extent and causes of this phenomenon.

The purpose of fruit inventories is to determine population level fruit yield. For this we need to multiply tree density with mean tree productivity. Quantifying and describing variability in both production and demographic data helps to enhance the accuracy and meaning of results. In our study high tree density in fields and villages coupled with fruit production figures meant that these land-use types delivered the highest yields. Plains and rocky outcrops had similar tree densities, but high fruit predation in rocky outcrops meant much lower mature fruit yields.

Peters (1996) suggests that enhancing recruitment of trees can have a much greater effect on future yield than trying to increase the productivity though silvicultural treatments. Baobabs are long lived trees and in arid environments may only start to produce fruit after 125 years (Swanepoel, 1993), so boosting recruitment now will only improve production in over 100 years. Needless to say removal of large quantities of seed may have negative consequences to the population in future. Thus to quantify the effects of fruit harvesting on recruitment we need to improve our understanding of what affects current recruitment rates such as seed viability, germination and seedling survival.

5. Conclusion

The capacity of trees to produce fruit did not differ significantly between land-use types. Trees in villages and fields tended to produce slightly more fruit than trees in plains, rocky outcrops and nature reserves. A greater proportion of medium-sized fruit were produced in all land-use types, except in villages where similar proportions of small and medium-sized fruit were found.

As predicted, baboons have a major impact, with up to 85% reduction in mature fruit production in nature reserves and rocky outcrops. This may have severe implications for recruitment and for the availability of fruit for human use.

It was predicted that larger trees would produce larger-sized fruit and a greater quantity of fruit than smaller trees, but the findings showed that fruit production fluctuated widely between size-classes with weak relationships between tree size (dbh and crown volume) and fruit production.

Fruit production differed significantly between sub-adult trees (<100 cm dbh), and adult trees (≥100 cm dbh) with fewer sub-adult trees producing fruit than adults. It is suggested that, in order to save time and cost, only trees ≥100 cm dbh should be enumerated in fruit inventories.

We found high inter-annual variability in fruit production with a two and a half fold difference between the highest and lowest year. We predicted that this would be linked to in-season rainfall, but we found that this was not so and suggest that rainfall in the preceding year might have a greater impact than the current year.

A high proportion of adult trees (41%) produced less than 5 fruit per year. These were called 'poor-producers' and were equated to 'male' trees as described in West Africa (Assogbadjo et al., 2008). Poor-producers were found in all size-classes and land-use types. The extent of this tendency in Africa should be investigated as it may reveal interesting patterns in the reproductive biology of baobabs.

Baobab fruit are harvested and sold commercially throughout Africa. The use of the resource is increasing rapidly as derivatives of the fruit become sought after in international markets. This study aimed to improve the understanding of baobab fruit production in Southern Africa and to permit easier management by users, managers and conservationists and greater sustainability of this important resource.

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Chapter 5

Submitted paper

Are there male and female baobabs (*Adansonia digitata* L.)? A study of phenology, flowering and fruit-set patterns in southern Africa

Abstract

Baobabs (*Adansonia digitata*) are hermaphrodite plants with both male and female reproductive structures in the same flower. Yet across Africa many people refer to 'male' and 'female' trees that produce few versus many fruit respectively. This poses an intriguing question as biologically, baobabs cannot be considered dioecious. The primary focus of this study was to describe the phenology, flowering and fruit-set patterns of baobabs. Results are used to explore reasons for the above anomaly. Flowering followed a steady-state pattern, lasting for 1-5 months with peak flowering in November. For adult trees, flower number (711±72 and 287±33) varied significantly between two sequential years, but not fruit-set (average of 20±4%). Tree size showed weak logarithmic trends with flower number (R^2=0.3830, P<0.0001), but not with fruit-set (R^2=0.0045, *P*=0.5081). Flower number and fruit-set did not vary between land-use types, but length of flowering did with village trees flowering for the longest period. Producer 'female' and poor-producer 'male' trees, did not differ in flowering phenology (number, timing and length of flowering) (*P*>0.05), but did show a significant difference in fruit-set over two sequential years (t_{75}=-5.6783, P<0.001; t_{75}=-5.5991, *P*<0.001). Mean fruit-set (over both years) for producers and poor-producers was 33.48±5.16% and 0.17±0.08 %, respectively. Mechanisms underlying this pattern are discussed in terms of tree age, environment, pollination, genetics and evolutionary biology.

Key words:

Excess flowering; inter-annual variation; leaf-flush; tree size; land-use type.

1. Introduction

Baobabs (*Adansonia digitata* L.) are hermaphrodite plants with cosexual flowers (Baum, 1995a). Female and male reproductive organs are large and conspicuous in the flowers and yet a surprising number of people, right across Africa, believe that there are separate male and female trees (Assogbadjo *et al*. 2008; Venter and Witkowski, unpublished data; Diana Mayne, Colin Bristow and Kemi NKaelang pers. comm.). Trees that produce fruit are referred to as 'female' and those that do not, as 'male'.

In West Africa, local people associate female baobabs with desirable traits such as delicious leaves, easy-to-harvest bark, sweet acidic non-slimy pulp and large good tasting kernels, whereas male trees are associated with slimy fruit pulp, tasteless kernels, bitter leaves and difficult-to-harvest bark (Assogbadjo *et al.*, 2008). In southern Africa, local people also distinguish between male and female trees. Interviews conducted with baobab

fruit harvesters revealed that 90% believed that there were male and female baobab trees (Venter and Witkowski, unpublished). Local African people and park rangers in both southern and East Africa regularly mention this phenomenon (Diana Mayne, Colin Bristow and Kemi NKaelang pers. comm.). Further published reports on male and female baobabs are not easy to find, probably because the idea is considered to be 'far-fetched' and so not often reported.

However, the results of a baobab fruit production study by Venter and Witkowski (2011) found that about 50% of adult trees hardly produced any fruit despite apparent normal flowering. These trees were termed 'poor-producers' and it was suggested that they might be likened to 'male' trees. The high prevalence of these trees in the population is intriguing.

Baobab (*Adansonia digitata*) flowering phenology has been described for a number of sites around Africa, however very little quantitative work has been published. Dhillion and Gustad (2004) and Assogbadjo *et al.* (2005) included phenological diagrams in their work in West Africa and Fenner (1980), Wickens (1982) and Swanepoel (1993) contributed personal observations from other parts of Africa. Von Breitenbach and Von Breitenbach (1974) spent a season enumerating the nocturnal opening of flowers on one tree in northern South Africa. These accounts indicate that baobab phenology varies across Africa with latitude and rainfall, but none offer information on between tree, environmental and inter-annual variation in flowering phenology.

A thorough and informative contribution on floral morphology comes from Baum (1995a). However, studies on other aspects of the reproductive biology are scarce with limited observations of bat pollination in West and East Africa (Baum, 1995a). To date, breeding system studies have not been done.

The aim of this study was to quantify baobab phenology, flowering and fruit-set in relation to intrinsic (tree size and life-stage) and extrinsic (environmental) factors. It was predicted that flowering and fruit-set would increase with tree size, that there would be differences between land-use types and that high inter-annual variation would be linked to rainfall patterns. Results are discussed in relation to baobab reproductive strategies and the various mechanisms that may result in 'male' trees.

The specific objectives of the study were:

1) Describe baobab phenology in South Africa.
2) Describe and quantify inter-annual variation in flowering and fruit-set for two sequential years.
3) Test the prediction that flowering and fruit-set increases with tree size (dbh).

4) Investigate how flowering and fruit-set differs between adult and sub-adult (<100cm dbh) life stages.
5) Compare fruit-set and flowering between land-use types.
6) Test whether 'producers' and 'poor-producers' differed in flowering and fruit-set.

2. Materials and methods

2.1 Study site

Research was conducted in northern South Africa (around 22°19'S and 30°28'E) an area commonly known as Northern Venda. The area is classed as semi-arid with a rainfall averaging between 334 and 423mm and a high coefficient of variation: 35-40% (Schulze, 1997). Summers (October-March) are characteristically hot and winters (April–September) are mild. Frost seldom occurs (Mucina and Rutherford, 2006). The average altitude of the region is 400 m above mean sea level and is underlain by sandstones of the Karoo Supergroup and the Clarens and Letaba Formations (Mucina and Rutherford, 2006). Soils are generally deep sands and shallow sandy lithosols (Mucina and Rutherford, 2006). It is part of the Zambezian Regional Centre of endemism where baobabs are associated with *Colophospermum mopane* (mopane) woodland (Wickens and Lowe, 2008). Bush fires are not common, due to low grass and herb biomass. Elephants are infrequent visitors. The area comprises communally managed land consisting of rangelands, fields and villages with two provincially managed nature reserves, Makhuya and Nwanedi, flaking the study area to the east and west respectively (Fig. 1).

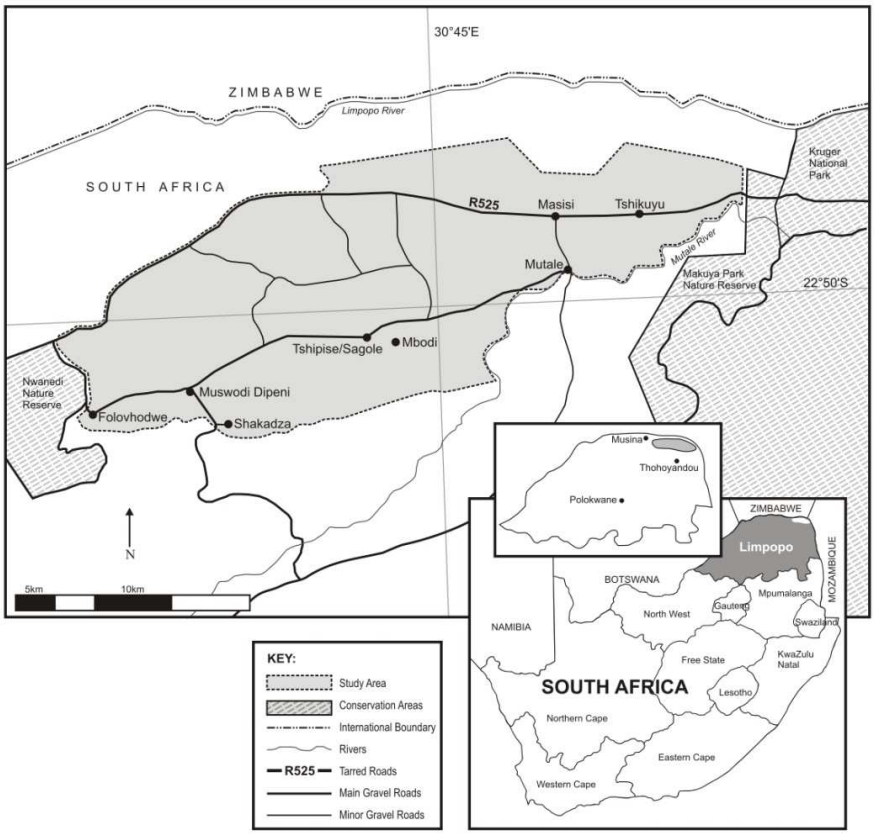

Figure 1. Map indicating location of study area in Limpopo Province, South Africa

2.2 Study species

Adansonia digitata is one of eight species of baobab in the genus *Adansonia* L. (Malvaceae, subfamily Bombacoideae) and the only one which naturally occurs on mainland Africa (Baum, 1995b). In South Africa the population is limited to the Limpopo River valley, with the exception of a few isolated trees found further south (Wickens and Lowe, 2008).

Phylogeographic research shows that the African baobab is tetraploid and may have evolved from a diploid ancestor originating in West Africa. Three distinct groups are found: two in West Africa and the third in southern and eastern Africa. Baobabs in southern and eastern Africa can be regarded as one phylogeographic population due to low genetic variation within this group (Tsy *et al.*, 2009).

Baobabs are known to be deciduous, bearing leaves and flowers in the wet season (Wickens, 1982; Baum, 1995a). Flowers are large (8 – 12 cm), white and pendulous with stigma, anthers and nectar spatially separated in the same flower. Anthesis usually occurs in the evening, with 10 – 15 flowers per tree opening synchronously each night. This takes place rapidly when the calyx, which completely encloses the flower bud, splits open and flexes back. Flowers abscise within 24 hours (Baum, 1995a). Stigma receptivity

commences at the time of anthesis and remains receptive until morning. Controlled hand pollination experiments on *Adansonia gregorii* (previously *A. gibbosa*) showed that *A. gregorii* are self-incompatible. Pollen tube growth in *A. gregorii* successfully penetrates the ovules, thus incompatibility is late acting (Baum, 1995a). No such study has been published for any other species in the genus, so it has been assumed that all species in the genus are obligate out-crossers. In well-watered environments such as gardens, trees grown from seed can start to flower from 22 years of age (Pardy, 1953). However, in their natural semi-arid environment, trees may only start flowering at 125-189 years of age (Swanepoel, 1993; A. Patrut, D. Mayne and S.M.Venter, unpublished data). The period between flowering and fruit ripening is usually 5-6 months (Sidibe and Williams, 2002). Seed production is substantial and viability percentages are high (>89%), but recruitment is limited by poor rainfall and herbivory (Venter & Witkowski, unpublished).

2.3 Sampling and measurement

Field work was done over two summer seasons, starting in October 2006 and ending in April 2008. Measurements were taken in five land-use types: 1) nature reserves; 2) plains; 3) rocky outcrops; 4) fields and 5) villages. Except for nature reserves, all of these represent different categories of communally-managed land. Trees were selected to include a wide range of stem diameters. Each tree was considered as a sample. In total, 106 trees were sampled, 34 in nature reserves and 18 in each of the other land-use types.

Geographic position (degrees latitude and longitude) and diameter at breast height (dbh, at 1.3m above the ground) was recorded for each tree. Each tree was assessed repeatedly for leaves, flowers and fruit at intervals of 1-2 months during two summer seasons (October 2006 - April 2008). For each assessment, the dominant leaf category was recorded as flushing, mature or dry. Flowers and fruit were counted. Fallen fruit were counted and then discarded, so that they would not be counted again. Fruit-set was determined as the percentage of fruit to flowers per tree. Rainfall and temperature records were sourced from the adjacent Kruger National Park and the Musina Weather Station.

In order to discount any obvious physical differences in male and female reproductive structures, 16 flowers were collected: 8 from ‘poor-producer’ trees and 8 from ‘producer’ trees. Flowers were immediately placed in ‘Kew Cocktail’ (73 parts Alcohol, 28 parts water, 1 part glycerine, 1 part formalin) for preservation. They were dissected, viewed and recorded at 8 times magnification, using a Leica EZ4 D stereo-microscope with an integral digital camera.

2.4 Data analysis

Phenological diagrams were constructed for each year, using the proportion of adult trees that were in leaf, flower and fruit each month. These were visually compared with rainfall and temperature variations to discern possible environmental cues.

The onset of flowering and leaf flush for each year was compared to each other and to the onset of rainfall by using the percentages of trees in flower and in leaf. To test if there were significant differences in the number of trees that flowered in November and December of each year, Cochran Q tests were used.

The total number of flowers (log transformed), length of flowering (months), percentage fruit-set (arcsine transformed) and proportion of flowering trees were compared between years using the Wilcoxon matched pairs test and the Cochran Q test. Data was combined for both years and ANOVA followed by Fishers Least Significant Difference (LSD) ($p < 0.05$) was used to test length of flowering against number of flowers (log transformed), number of fruit (log transformed), fruit-set (arcsine transformed) and tree size (dbh). For this analysis only 2, 3 and 4 month data was used because the few trees that flowered for 1 month (3 trees) and for 5 months (5 trees) exhibited high variability.

Population peak flowering was defined as >50% of adult trees in flower in a calendar month. For individual trees, a peak flowering month was defined as the month in which the tree produced the largest number of flowers compared to other months. These were depicted graphically against rainfall. Differences in flower number (log transformed), fruit number (log transformed) and fruit-set (arcsine transformed) of trees that had peaked in different calendar months within each year were analysed using t-tests and ANOVA. November was considered a peak flowering month, so, to test if this was consistent between years, the Cochran Q test was used.

The proportion of adult trees falling into each flower class (0-4, 5-49, 50-199, 200-399, 400-599, 600-799, 800-999, 1000-1499, ≥1500 flowers/tree) and fruit-set class (0%, 0.1-0.9%, 1-19%, 20-39%, 40-59%, 60-79%, 80-100% fruit set/tree) was illustrated. Further figures show average fruit-set and fruit number per flower class. Regression analysis tested the relationship between flower number and fruit-set. Diameter at breast height (dbh) was chosen as an indicator of tree size because it is well related to crown size ($R^2 = 0.5904$) (Venter and Witkowski, 2011). Regression analysis determined if flowering and fruit-set increased with dbh. Size-class distributions of flowers per tree were constructed for each year and for both years combined. This allowed for visual comparisons and to test for differences between years using Kolmogorov-Smirnov tests. Trees were divided into sub-adult (<100 cm dbh) and adult (≥100 cm dbh) life-stages, (Venter and Witkowski, 2011) and the difference in numbers of flowers (log transformed) and fruit-set (arcsine transformed) between life-stages within each year was tested using t-tests. Differences between years in

flowering, fruit-set and number of flowering trees was tested using the Wilcoxon matched pairs test and the Cochran Q test.

Differences between land-use types in number of flowers (log transformed), length of flowering and fruit-set (arcsine transformed) were compared over both years using ANOVA followed by Fisher's LSD (p <0.05).

Using t-tests, trees that were classed as 'poor-producers', based on producing <5 fruit per year (Venter and Witkowski, 2011), were compared to 'producers', for flower number (log transformed), length of flowering and fruit-set (arcsine transformed). Regression analysis tested the relationship between flowering and fruit-set for 'producers' and 'poor-producers' separately.

3. Results

3.1 Phenology and flowering patterns

Baobabs followed a steady-state flowering pattern with flowering starting in November (2006) and October (2007) and continuing until April in both years (Fig. 2).

Leaf flush responded more quickly to early rain than did flowering (Fig. 2). In the first year, trees flowered and flushed leaves at the same time, whereas in the second year trees flushed leaves one month earlier than flowering (Table 1).

Flowering between years was compared for October, November and December. In October 2006 no trees flowered, whereas in October 2007 75% had started flowering. There was no significant difference in the number of trees that flowered in November of each year ($Q = 2.0000$, $P = 0.1573$). However, significantly more trees flowered in December 2006 than December 2007 ($Q = 16.1333$, $P <0.0001$) (Fig. 4C and 4D). This is possibly due to the later start of the flowering season in 2006. Adult trees flowered for significantly longer in 2007 than 2006 ($Z = 2.8996$, $P = 0.0037$) (Fig. 3B). In both years flowering decreased in January and stopped in April, but in 2006 10% more trees continued to flower during the late summer season (January – April) possibly in response to in season rainfall events (Fig. 4C and 4D). Trees that flowered for 4 months produced significantly more flowers than trees that flowered for 2 and 3 months ($F_{2,144} = 4.7959$, $P = 0.0096$) (Fig. 4A). Population peak flowering differed between years, although the majority of trees peak-flowered in November in both years ($Q = 0.0265$, $P = 0.8728$) (Fig. 3A). In 2006, trees peak-flowered for two months, November and December and in 2007 for three months, October, November and December (Fig. 3A). Trees that peak-flowered in different months of the same year did not differ in number of flowers produced (2006: $t_{75}=0.7335$, $P=0.4656$; 2007: $F_{(2,75)=}1.1102$, $P=0.3348$). The proportion of adult trees (>100 cm dbh) per flower production class (Fig. 5A) had a positively skewed distribution, the majority of adult trees (53%) produced between

200 – 599 flowers. Nine percent produced >1000 flowers per year, and 4% produced <49 flowers per year (Fig. 5A).

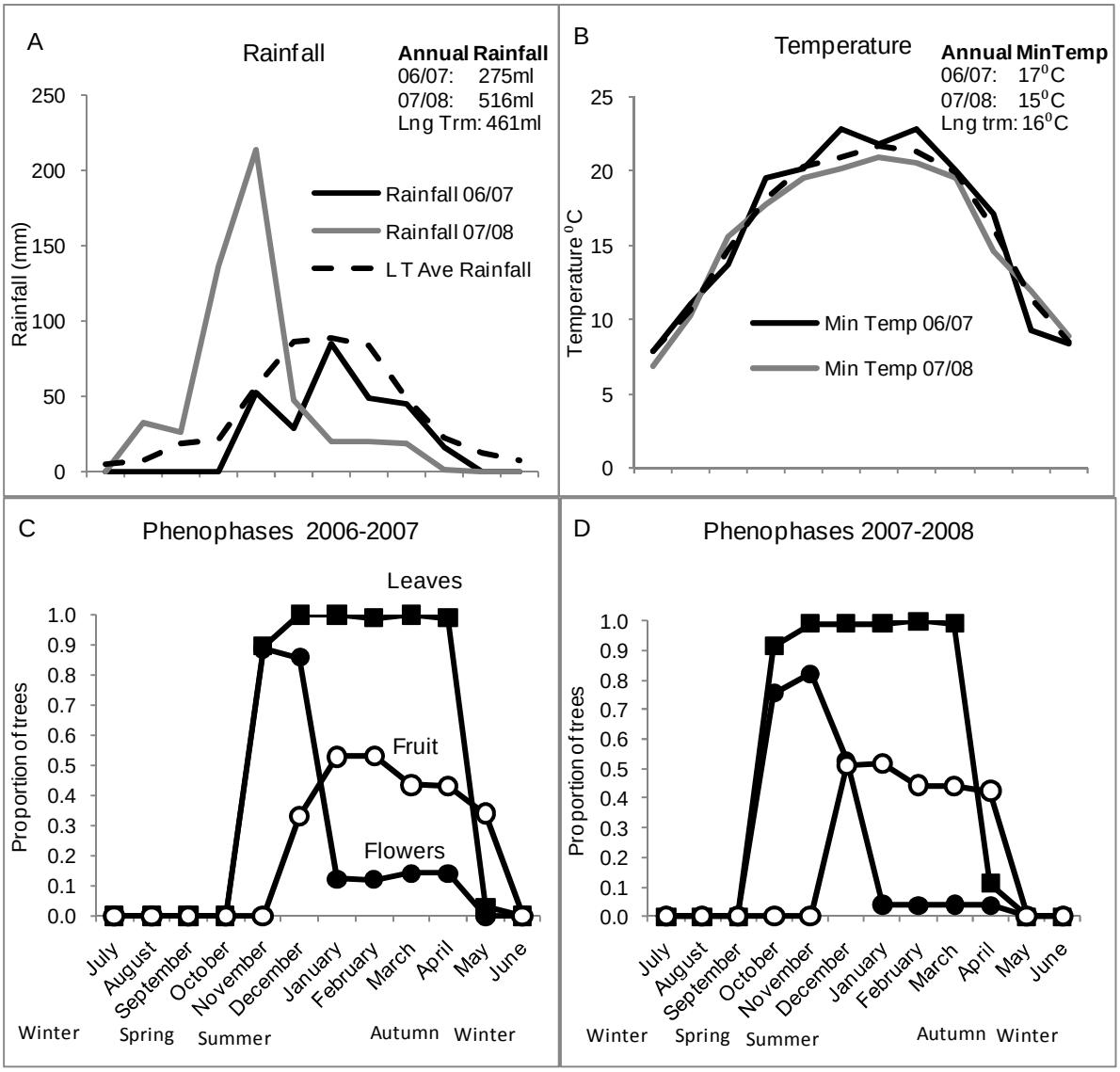

Figure 2. Monthly rainfall for 2006 - 2007 and 2007 - 2008 and the long-term (80 yr) average (A). Monthly minimum temperature for 2006 - 2007 and 2007 - 2008 and the long-term (19 yr) average (B). Proportion of *Adansonia digitata* trees in 2006 - 2007 (C) and 2007 - 2008 (D) that were in leaf (filled squares) and which had flowers (filled circles) and fruit (open circles) each month (n = 106).

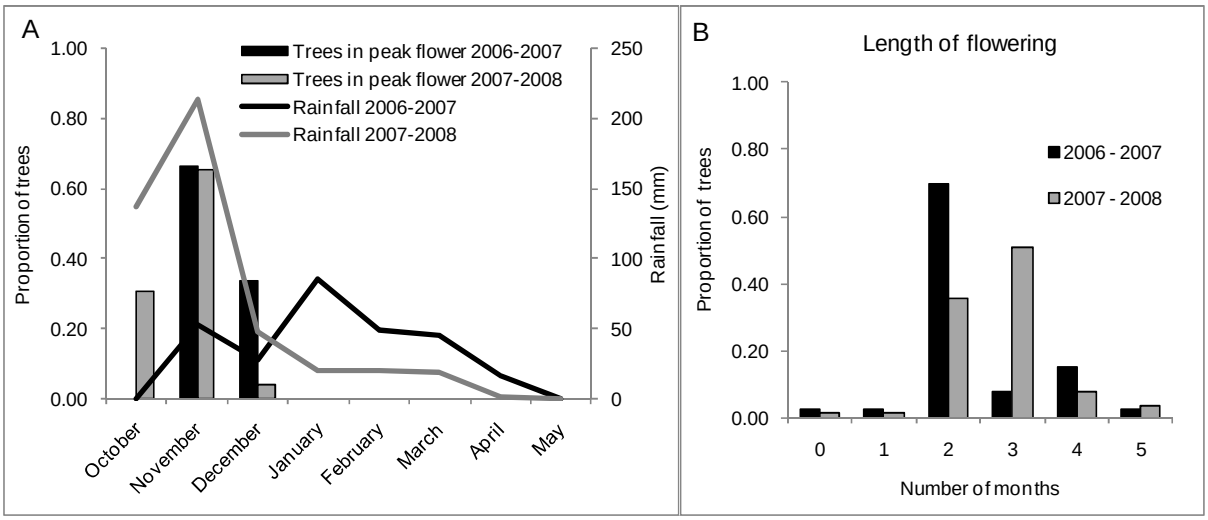

Figure 3. Proportion of adult trees (n=79) exhibiting peak flowering in the 2006-2007 season (black bars) and 2007-2008 season (grey bars) and monthly rainfall each season (A). Proportion of trees flowering for different lengths of time each season, 2006 - 2007 (black bars) and 2007 - 2008 (grey bars) (B).

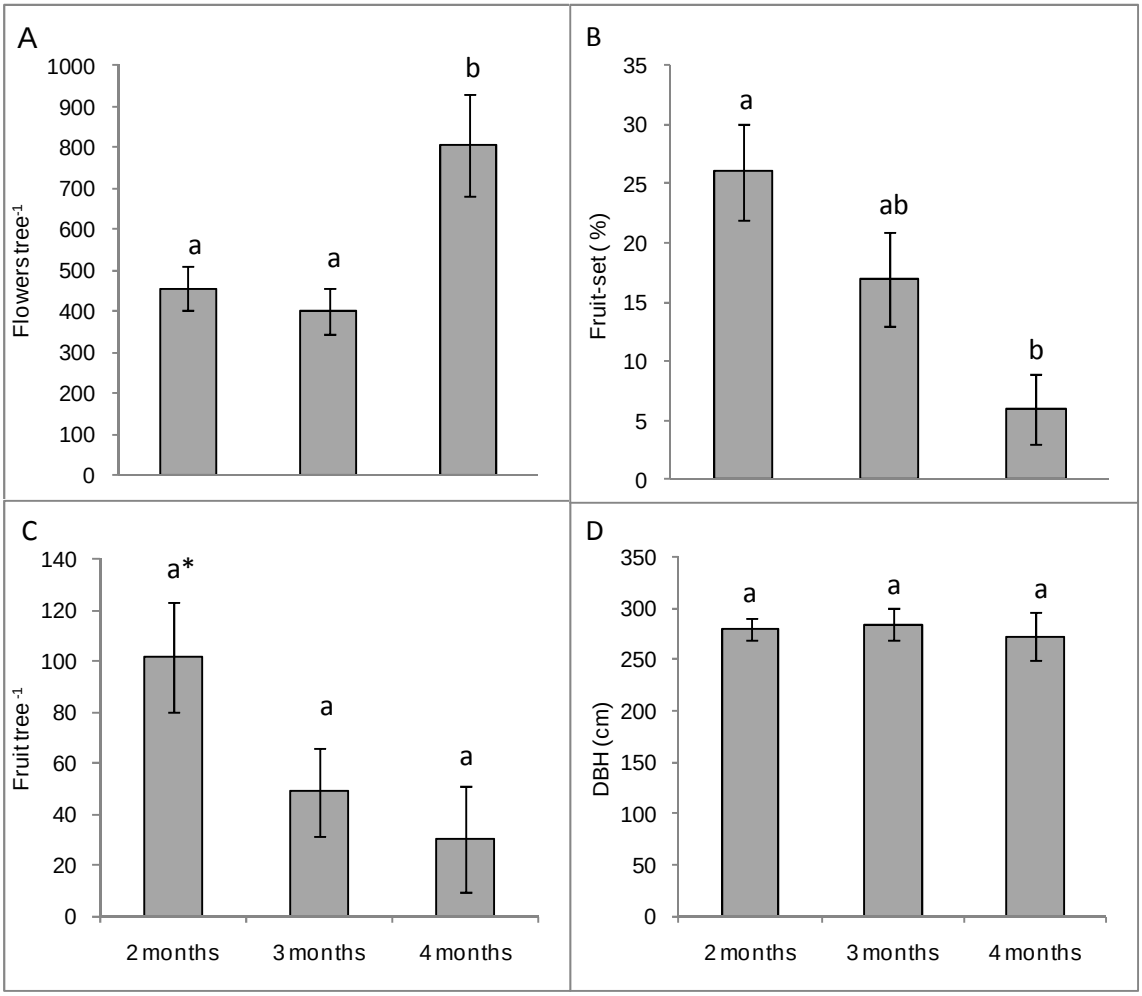

Figure 4. Length of flowering per tree versus number of flowers per tree (A), fruit-set per tree (B), number of fruit per tree (C) and tree size (cm dbh) (D) (mean ± SE). Trees were sampled over two consecutive years and results combined. 1 and 5 month categories excluded due to small sample sizes. Lower-case letters (a,b) indicate significant differences. a* indicates that t-test, between individual bars, shows significant difference ($p < 0.05$).

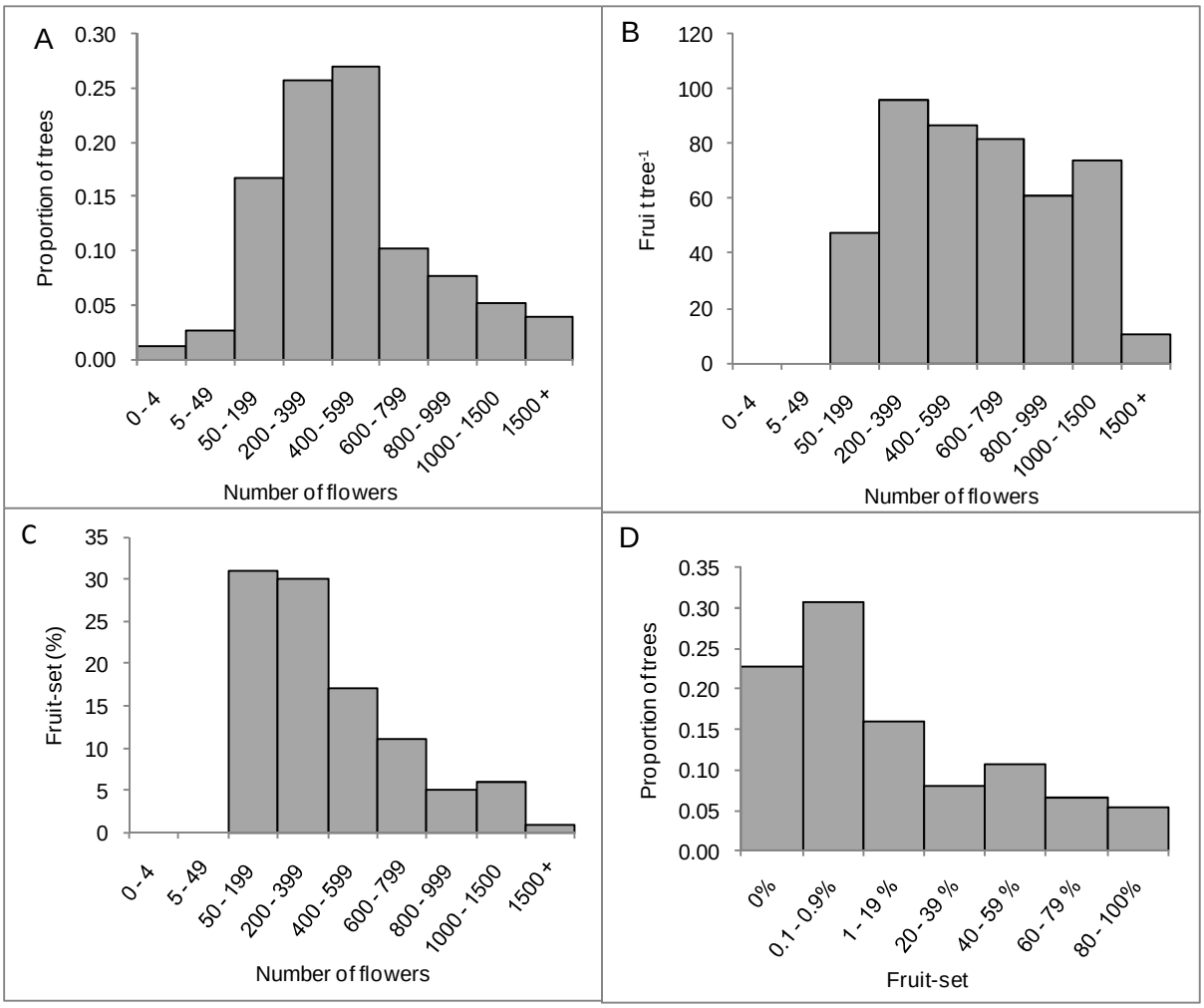

Figure 5. Proportion of adult trees (A), number of fruit (B) and fruit set per flower-class (C) as well as the proportion of trees per fruit-set-class (D) (n = 79).

Table 1. Percentage of trees that are in leaf and in flower in relation to the onset of rainfall and leaf flush each year (n = 106).

Year (July - June)	Leaf flush preceeds rain (% of trees)	Flowering preceeds rain (% of trees)	Flowering preceeds leaf flush (% of trees)	Flowering and leaf flush at the same time (% of trees)	Leaf flush preceeds flowering (% of trees)
Year 2006- 2007	88%	84%	5%	54%	42%
Year 2007 - 2008	0%	0%	3%	39%	59%

3.2 Fruit-set and fruit production patterns

Trees that peak-flowered in different months of the flowering season did not differ in fruit-set (2006: t_{75}=-0.7264, *P*=0.4689; 2007: $F_{(2,75)=}$1.6885, *P*=0.1918) or fruit production (2006: t_{75}=-0.4459, *P*=0.6569; 2007: $F_{(2,75)=}$1.7541, *P*=0.1801).

Adult trees that produced between 50 – 400 flowers had the highest average fruit-set of 30%. After this, fruit-set declined with flower number (Fig. 5C). Trees that produced >1500 flowers had a fruit-set of <1%. This explains why trees that had 200 – 1500 flowers produced similar amount of fruit (Fig. 5B), with the exception of trees that produced >1500 flowers; these trees, by contrast, produced very few fruit. On the other hand, adult trees that produced <50 flowers did not produce any fruit and may have been compromised by the environment. Regression analysis (excluding trees with <50 flowers) shows a weak negative trend between flower number and fruit-set (R^2 = 0.0973, *P* = 0.0065) confirming the negative trend in Fig. 5C. Figure 5D shows that the proportion of trees, per fruit-set class, had an inverse J-shaped distribution with 23% of adult trees not setting fruit at all, and 31% with fruit-set of <1%. Fruit-set decreased with an increase in flowering time ($F_{2,144}$ = 3.6770, *P* = 0.0277) (Fig. 4B). However, fruit production did not differ significantly between flowering periods ($F_{2,144}$ = 1378, *P* = 0.2562). Declining fruit-set may have counteracted the increase in flower number, thus evening out fruit production against length of flowering (Fig. 4).

3.3 Tree size in relation to flowering and fruit-set

Regression analysis showed that there were weak logarithmic trends between dbh and flowering (R^2 = 0.3830, *P* < 0.0001), and no trend between dbh and fruit-set (R^2 = 0.0045, *P* = 0.5081). Neither length of flowering (Fig. 4D) nor timing of peak flowering differed with tree size ($F_{2,146}$ = 0.0814, *P* = 0.9218; $F_{2,152}$ = 0.4636, *P* = 0.9541).

3.4 Inter-annual variation

There was a significant difference between years in the number of flowers produced by adult trees (Z = 5.4613, *P* < 0.0001) (Table 2). The shape of the size-class distribution for flower production did not differ between years, which means that all trees, regardless of size, produced fewer flowers in the second year (D = 0.09, *P* >0.05) (Fig. 6). There was no significant difference in fruit-set between the years (Z = 0.6141, *P* = 0.5391) (Table 2). This implies that fruit production was determined by the number of flowers produced and not by reduction in fruit-set. Furthermore, the number of adult flowering trees did not differ between years (Q = 1, *P* = 0.3173) (Table 2).

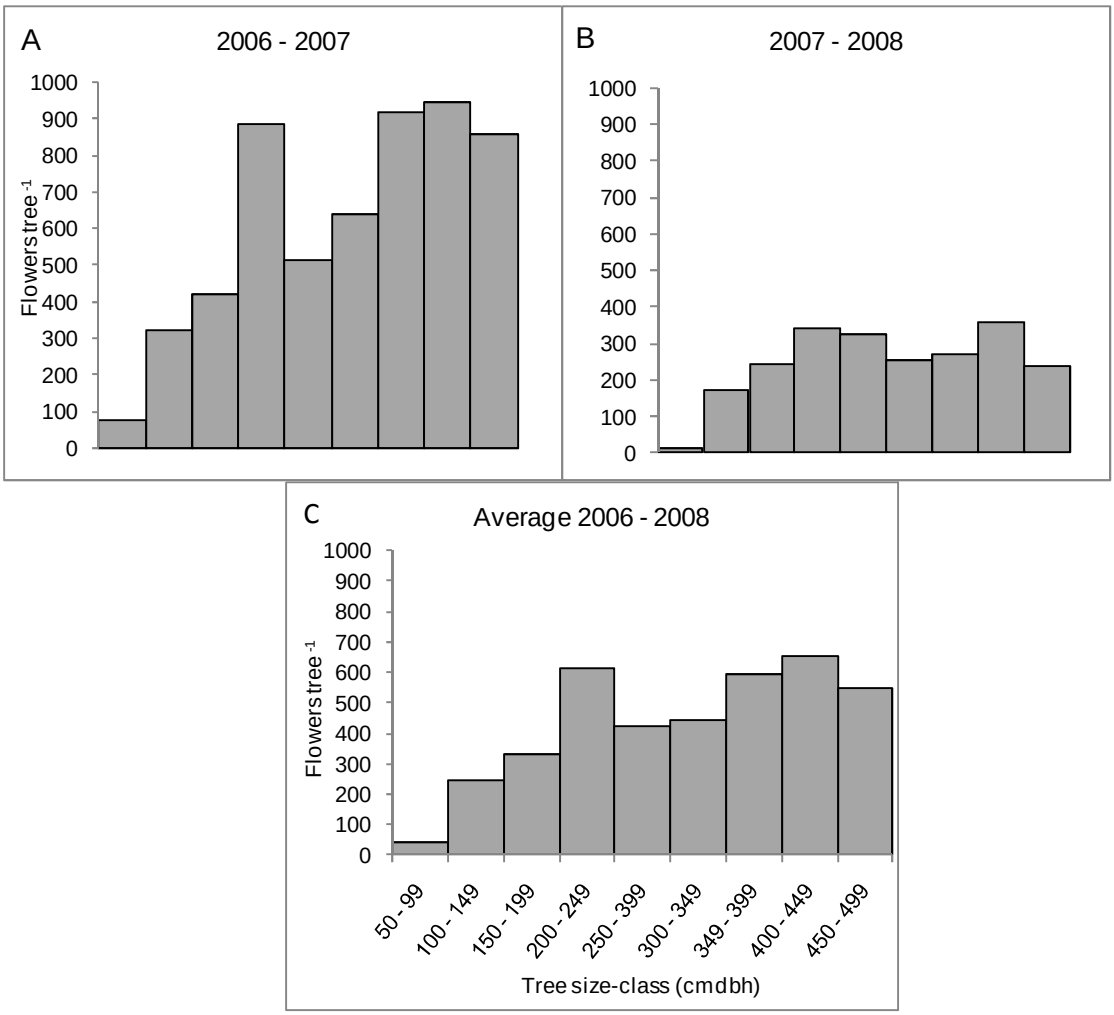

Figure 6. Mean flower production per tree size-class for each season: 2006 - 2007 (A), 2007 - 2008 (B) and the average over both seasons (C) (n = 106).

Table 2. Flowers per tree and fruit-set per tree in sub-adult and adult life stages in 2006 - 2007 and 2007 - 2008 and the average over both years, as well as number of trees in flower between years within each life stage. Flower numbers were Log transformed and fruit-set arcsine transformed for analysis. Fruit-set was determined only from trees that produced flowers, hence the differences in df.

	Year	Sub Adult	Adult	t	*P*
		mean ± SE	mean ± SE	Between Life stages (a,b)	Between Life stages (a,b)
Flowers/tree	2006-2007	75.52 ± 21.30^{aA}	710.86 ± 72.73^{bA}	$t_{104} = -8.3134$	$P < 0.001$
	2007-2008	12.41 ± 5.15^{aB}	287.27 ± 32.91^{bB}	$t_{104} = -12.3097$	$P < 0.001$
	Ave both Years	43.96 ± 12.59^{a}	499.06 ± 45.11^{b}	$t_{104} = -10.3675$	$P < 0.001$
Fruit-set /tree	2006-2007	14.22 ± 7.92^{aA}	19.91 ± 3.54^{aA}	$t_{95} = -0.5915$	$P = 0.5555$
	2007-2008	21.26 ± 9.16^{aA}	20.23 ± 3.67^{aA}	$t_{88} = 0.1848$	$P = 0.8538$
	Ave both Years	$17.76 \pm 8.31\ \%^{a}$	$20.07 \pm 3.61\ \%^{a}$	$t_{96} = -0.4177$	$P = 0.6771$
Number of flowering trees	2006-2007	20^{A}	77^{A}		
	2007-2008	12^{B}	78^{A}		

Lower case letters (a,b) indicate differences between life stages in rows and capital letters (A,B) indicate differences within each life stage between years

3.5 Life-stage

Trees <100cm dbh produced significantly fewer flowers, but did not have significantly lower fruit-set than trees ≥100 cm dbh (Table 2). Sub-adults produced significantly more flowers in 2007-2008 than in 2006-2007 ($Z = 3.8826$, $P < 0.0001$) (Table 2). Fruit-set did not differ significantly between years ($Z = 1.2602$, $P = 0.2067$) (Table 2). A significantly different number of sub-adult trees flowered each year ($Q = 8$, $P = 0.0047$) (Table 2).

3.6 Land-use type

There were no differences in flower number ($F_{4,150} = 1.5133$, $P = 0.2011$) or in fruit-set ($F_{4,150} = 0.8419$, $P = 0.5006$) between land-use types over both years. However trees in villages tended to produce more flowers and flower for significantly longer ($F_{4,150} = 6.4694$, $P < 0.0001$) than in other land-use types.

3.7 Producers versus poor producers

There was no significant difference in the number of flowers produced by 'poor-producers' versus 'producers' (Table 3). The same number of 'poor-producing' trees flowered each year and for 'producers' only one more tree flowered in the second year compared to the first (Table 3). Similarly length of flowering did not vary between 'producers' and 'poor-producers' for either of the two years (2006-2007: $t = -0.6837$, $P = 0.4962$; 2007-2008: $t = 0.1359$, $P = 0.8923$). Fruit-set, however, differed significantly between 'poor-producer' and 'producer' categories (Table 3). 'Poor-producers' had an average fruit-set of 0.17% and 'producers' an average fruit-set of 33.48%. Regression

analysis showed that for 'producers' fruit-set declined with an increase in flower number (R^2 = 0.2486, *P* = 0.0004) and for 'poor-producers' fruit-set did not change with flower number (R^2 = 0.0039, *P* = 0.7395).

Dissected flowers showed no obvious morphological differences in floral reproductive structures. All flowers had intact female and male reproductive parts.

Table 3. Flowers and fruit-set per tree for poor-producer and producer categories in 2006 - 2007 and 2007 - 2008 and the average over both years, as well as the number of trees in flower between years within each category. Flower numbers were Log transformed and fruit-set arcsine transformed for analysis. Fruit-set was determined only from trees that produced flowers, hence the differences in df.

	Year	Poor-producer mean ± SE	Producer mean ± SE	t	*P*
Flowers/tree	2006-2007	592.37 ± 98.72[a]	791.53± 101.28[a]	t_{77} = 1.8020	*P* = 0.2834
	2007-2008	310.56 ± 60.73[a]	271.40 ± 37.18[a]	t_{77} = 0.1497	*P* = 0.8814
	Ave both Years	451.47 ± 65.74[a]	531.47 ± 61.32[a]	t_{77} = 1.0658	*P* = 0.2898
Fruit-set /tree	2006-2007	0.20 ± 0.07 %[a]	33.20 ± 5.07 %[b]	t_{75} = -5.6783	*P* < 0.001
	2007-2008	0.14 ± 0.09 %[a]	33.77 ± 5.28 %[b]	t_{75} = -5.5991	*P* < 0.001
	Ave both Years	0.17 ± 0.08 %[a]	33.48 ± 5.16 %[b]	t_{75} = -6.1924	*P* < 0.001
Number of flowering trees	2006-2007	31	46		
	2007-2008	32	46		

Lower case letters (a,b) indicate differences between columns

4. Discussion

4.1 Phenology

Rainfall, temperature and day-length are important variables in determining leaf flush in arid savanna ecosystems (Chidumayo, 2001; Archibald and Scholes, 2007). For trees that flush leaves before the onset of rains, day length and temperature determine the initiation of leaf flush (Borchert and Rivera, 2001; Archibald and Scholes, 2007). This suggests that trees which flush leaves before rains are more deterministic in their behaviour, accepting the risk of poor growing seasons in order to take advantage of a number of factors, such as the pulse of nutrients which are released with the onset of first rain, minimal insect activity and high irradiance in order to be ready to photosynthesize (Wright and Schaik van, 1994; Archibald and Scholes, 2007).

Baobab leaf flush is presumably initiated by day-length and temperature, the trees generally flush leaves prior to the onset of the rainy season (Fenner, 1980; Swanepoel, 1993; Chapotin *et al.*, 2006). Baobabs use stored stem water to flush new leaves, but not to support stomatal opening, which only occurs after the first good rain (Chapotin *et al.*, 2006).

Early leaf flush allows trees to take advantage of early or scattered rain events (Chapotin *et al.*, 2006). When exceptionally early rains fell in 2007, leaf flush occurred after the onset of rains, but also earlier than in 2006, which was regarded as a normal rainfall year. Hence, early rainfall may have overridden the day-length/temperature cues, resulting in trees flushing leaves earlier than usual in that year.

Poor stem water and limited nutrient reserves from a previous, unfavourable, growing season may influence the capacity of trees to produce flowers and fruit in the current season, despite better conditions (Witkowski, 1990). This may explain poor flower and fruit production in the second season (2007-2008), despite having almost double the rainfall than the previous season (2006-2007), when rainfall had been below average. Fruit production increased again in 2008-2009 (Venter and Witkowski, 2011), possibly due to the previous season's above average rains which allowed trees to build up reserves.

Flowering can also start before the onset of rains and, like leaf-flush, is probably supported by stem-water reserves. Even though timing varied between years, peak flowering still occurred in November of each year. This supports the notion that a deterministic mechanism, such as day-length or temperature, and not rainfall, cues baobab flowering (Gentry, 1974; Rathcke and Lacey, 1985).

Baobab flowering exhibits sufficient variation in length of flowering and peak flowering period for it to be under relaxed selection pressure (Ollerton and Lack, 1992). This allows the population more flexibility in its responses to changes in the environment, and to respond to possible stronger selection pressures in future. Fruit-set is not affected by the timing of individual flowering peaks, nor by land-use, suggesting that pollination is not strictly limited in time and that plants do not require very specific resources in order to set fruit successfully. One may conclude, therefore, that its flexible flowering phenology allows baobabs to be more resilient to environmental fluctuations.

4.2 Reproductive strategy

4.2.1 Excess flower *production*

The production of excess flowers is common in hermaphrodite plants (Sutherland and Delph, 1984). It is hypothesized that this has a number of advantages, including bet-hedging, allocation to male fitness (pollen donation) and allocation to female fitness (selective abortion) (Sutherland and Delph, 1984; Ayre and Whelan, 1989).

Baobabs exhibit a steady-state flowering pattern (Gentry, 1974) which lasts for one to five months. We found that fruit-set and fruit production did not differ between trees that peak-flowered in different months, suggesting that baobabs are well adapted to cope with unpredictable flowering seasons without a loss in fecundity. This allows trees to invest in a

form of bet-hedging. The advantage of such a strategy is to spread over a longer time, the risk of poor environmental conditions and unpredictable pollinators (Zimmerman, 1988).

A further advantage of a steady-state flowering pattern is that it achieves higher out-crossing. Plants with few flowers produced over a longer time have a better chance of outcrossing than plants that produce all their flowers together, adopting a 'big bang' strategy (Richards, 1986). Furthermore, plants that flower late in the season achieve higher out-crossing than plants that flower in peak season (Zimmerman, 1988). This is because there are fewer available pollinators, and pollinators have to travel greater distances to reach flowers and thus move pollen further (Zimmerman, 1988). Thus a steady-state flower strategy could enhance out-crossing in baobabs.

Sutherland and Delph (1984) argue that an excess in flower production increases male fitness, because plants produce flowers that function solely as pollen donors. Fruit and seed production (female functions) are more costly than pollen production (male function), therefore, in order to balance the investment in male and female functions, plants should produce more flowers than fruit. Charnov (1979) argued that sex allocation is an evolutionary stable strategy (ESS) that depends on the shape of the fitness-gain curves relating to female and male fertility functions. The production of excess flowers in baobabs may therefore be an investment in male function, as argued for other species (Sutherland, 1987; Ayre and Whelan, 1989).

Burd (1998) hypothesized that 'excess' flower production may also increase female fitness by allowing selective maturation of fruit of superior quality. In resource limited environments, maternal plants are known to allocate a disproportionate amount of nitrogen and phosphorus to seeds in order to ensure successful seedling establishment (Witkowski and Lamont, 1996). Baobab recruitment is highly episodic (Venter and Witkowski, 2010), so investment in good quality seed (Venter and Witkowski, unpublished) may be very important for this species. The study area is also resource poor – low rainfall and generally poor sandy soils.

Excess flower production also increases female fitness by allowing the plant to rapidly adjust fruit-set when conditions improve (Witkowski, 1990; De Jong and Klinkhamer, 2005). However, in baobabs, annual variation in fruit production was linked to a reduction in the number of flowers rather than to a reduction in fruit-set. This means that female fitness was not a post-fertilization decision, as suggested above, but a pre-fertilization decision. The decision to produce fewer flowers, presumably influenced by a lack of resources, would affect both male and female fitness.

4.2.2 Poor producers or ‘male’ trees

Bet-hedging and allocation to male and female fitness through pollen donation and ovule abortion may be the reason for excess flower production in ‘producers’, but these alone do not explain poor fruit-set in ‘poor-producers’. The almost complete lack of fruit production in ‘poor-producers’ remains interesting. We found no difference in flowering phenology (flower production, length of flowering, peak flowering), but a substantial difference in fruit-set between these categories, with ‘poor-producers’ (0.17%) having significantly lower fruit-set than ‘producers’ (33%). Low fruit-set can occur for a number of reasons and these include 1) plant age 2) environment, 3) inadequate pollination, 4) genetic aberrations and 5) sexual dimorphism.

Size-dependent and environment-dependent sex allocation can occur in the form of diphasy, where small adult trees and adult trees in poor environments could be said to be like males, which switch to being ‘female’ once they are bigger, and trees in nutrient rich environments are ‘female’ (Schlessmann, 1988; De Jong and Klinkhamer, 2005). Our results showed that there was no difference in fruit-set between size-classes (age) or land-use type (environment). An increase in fruit production with tree size was a result of an increase in flowers production and not fruit-set. Furthermore, although trees in villages flowered for longer and tended to produce more flowers than trees in other land-use types, fruit-set did not differ from other land-use types. In addition, field observations indicate that soil and climate conditions did not influence fruit-set as ‘poor-producer’ and ‘producer’ trees were often found only a few meters apart within very uniform environments. Thus poor fruit-set, in this case, does not appear to be a function of age or environment.

Pollen limitation, both in terms of quantity and quality, has an influence on fruit-set (Aizen and Harder, 2007). Inadequate quantities of pollen are known to severely limit fruit-set especially when pollinators are scarce (Johnson *et al.*, 2004). Poor pollen quality, particularly in late acting self-incompatible species, such as baobab, disables ovules resulting in poor fruit-set (Aizen and Harder, 2007). Baobab flowers are known to be fruit-bat pollinated, however this has not been observed in southern Africa and field observations (S.M Venter, unpublished data) suggest that insects (hymenoptera spp.) may be playing an important role as pollinators in this area. However, flowers may not be adapted to insect pollination and many trees may be receiving a large amount of self pollen or pollen from closely related trees. However, this does not explain poor fruit-set in the same individual trees over multiple years, especially where they occur among trees that are good producers.

Low fruit-set may also be controlled on a genetic level. In polyploid species, infertility may be caused by meiotic aberrations, which is the most common cause of sterility in polyploids, and is known to result in semi-sterile adults (Ramsey and Schemske, 2002). Although a steady-state flowering pattern reduces inbreeding, the chance of geitonogamous

self pollination cannot be excluded, especially in mass flowering species. This can lead to inbreeding depression and low fruit-set.

Low fruit-set may also reflect a form of sexual dimorphism (Wilson, 1994). A gradual increase in gender specialization may be seen as a pathway to dioecy (Barrett, 2002). Barrett (2002) suggests that plant gender should be seen more from a functional rather than a morphological perspective and it is suggested that evolution of sex chromosomes may follow once dioecy is established (Charlesworth and Guttman, 1999). Hormonal controls on certain loci are able to modify sex expression that shift the balance between male and female expression (Charlesworth and Guttman, 1999). Such loci would increase sterility effects and development 'decisions' between male and female functions (Meagher, 1988). Baobabs have relatively low diversity across large geographic areas (Baum *et al.*, 1998; Tsy *et al.*, 2009), but high diversity within populations (Assogbadjo *et al.*, 2010) with high levels of polymorphism and polysomic inheritance (Assogbadjo *et al.*, 2006; Assogbadjo *et al.*, 2009; Larsen *et al.*, 2009). This makes identifying genetic markers for morphological variation and sexual behaviour complex but it also allows for evolutionary change to take place (Wilson, 1994). However, Pannell (2002) argues that plant populations that are 'cryptically dioecious' still need to make equal contributions to male and female function, therefore if 'poor-producers' are 'functionally male' then 'producer' should be 'functionally female' and not hermaphrodite. To assess if baobabs are 'cryptically dioecious' the paternal and maternal contribution of both categories of trees would need to be established.

5. Conclusion

Baobab flowering exhibits a steady-state pattern. Peak flowering occurs at the same time each year, suggesting that flowering is more strongly determined by day-length or temperature than by leaf flush. Flowering and fruit production are highly variable between years, and may be influenced by the previous season's conditions. There was a significant difference between the number of flowers produced between years, but no significant difference in fruit-set. Thus it would seem that variation in fruit production between years is a consequence of reduced flower production and not the capacity of the trees to set fruit. Likewise, flowering, not fruit-set, increased with tree size and life-stage, thus fruit production is influenced by increases in flowers and not fruit-set. Neither did fruit-set differ between land-use types although trees in villages flowered for longer and tended to produce more flowers than trees in other land-use types. Lastly, 'producers' and 'poor-producers' did not differ in flowering phenology but did differ significantly in fruit-set.

The results of this study show that the common belief that there are distinct 'male' and 'female' baobabs may not be as far-fetched as previously thought. Investigations into

the mechanisms that determine these patterns are required. DNA level, pollination and breeding system studies would help establish if low fruit production in 'male trees' is a result of poor pollination, self-incompatibility or female sterility. Exploring the idea of 'male' trees, may initially seem fanciful, but such ideas encourage observation and provide opportunities for hypotheses to be tested (Huxley, 1898 cited in Wilson, 1994).

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Chapter 6

Submitted paper

Where are the young baobabs? Factors affecting regeneration of *Adansonia digitata* L. in a communally managed region of southern Africa.

Abstract

Large baobabs are prominent in many African savannas, but the apparent lack of young trees suggests that recruitment is limited and possibly episodic. This study aims to determine if recruitment was seed or establishment (microsite) limited. From five annual seed crops, baobab seed consistently exhibit high viability (>89%) and a field trial shows they form persistent soil seed banks. Seed production is substantial (5500±2334 seed/ha) and thus recruitment does not appear to be seed limited, except possibly in areas where baboon predation of immature fruit is common. In closed plots (excluding livestock) 6.33% of seeds emerged after 328±28 (mean±SE) days and of these 94.4% died within 21±5 days of moisture stress and insect browsing. In open plots 2% of seeds emerged after 377±5 days and all of them died within 12±5 days from goat browsing. Planted sapling survival in closed plots (65%) was significantly better than in open plots (10%), with an average time to death of 10.45±0.97 and 4.33±0.45 months respectively. Hence poor seedling establishment, resulting primarily from infrequent rainfall, is typically episodic in baobabs and high livestock numbers further hamper recruitment. Active planting/protection of young trees from livestock is required to overcome the recruitment bottleneck.

Key words

Baboons; browsing; livestock; recruitment; regeneration ecology; trampling.

1. Introduction

Baobabs (*Adansonia digitata* L.) are large, distinctive, iconic trees, and the only species of the genus that is found on the African continent (Baum, 1995a). Across the continent, baobab trees are utilized for a wide variety of products including food, fiber and medicine and in this way provide an invaluable resource to many rural people (Sidibe and Williams, 2002). It is thus essential that the resource is managed sustainably to ensure its long-term persistence and productivity.

Poor baobab recruitment is commonly reported for many landscapes across Africa with many populations having bell-shaped or positively skewed stem diameter size-class distribution (SCD) curves (Hofmeyr, 2003; Dhillion and Gustad, 2004; Assogbadjo *et al.*, 2005; Chirwa *et al.*, 2006; Edkins *et al.*, 2007; Venter and Witkowski, 2010). In surveys done by Chirwa *et al.* (2006) in Malawi, Hofmeyr (2003) in the Kruger National Park and Venter and Witkowski (2010) in South Africa, no baobab seedlings were found. In West

African villages baobab seedlings are planted and actively protected from livestock, but outside villages there is poor recruitment (Dhillion and Gustad, 2004; Assogbadjo *et al.*, 2005). In South Africa, Venter and Witkowski (2011a) found fewer juvenile and sub-adult (<100 cm dbh) relative to adult baobabs in human-modified areas (villages and fields) than in adjacent more natural areas (plains and rocky outcrops). Here, unlike West Africa, baobab seedlings are not actively planted or protected (pers. obs.). The apparent lack of young baobabs in many populations has repeatedly led to the often-asked question, "where are the young baobabs?"

A wide range of variables can affect the success of baobab recruitment. Recruitment could be 1) seed limited, i.e. not enough viable seed available; or 2) establishment (microsite) limited, where emerging seedlings do not survive because of external factors associated with its environment (Eriksson and Ehrlen, 1992; Clarke *et al.*, 1998).

In general annual baobab fruit production is substantial, even though it varies considerably from year to year (Assogbadjo *et al*, 2005; Venter and Witkowski, 2011b). Nonetheless, little is known about the viability and persistence of seeds within natural or human-modified environments, or the factors that limit seedling establishment (Wilson and Witkowski, 1998).

Percentage germination of *A. digitata* seeds under nursery conditions ranges from 20-57% (Danthu *et al.*, 1995; Assogbadjo *et al.*, 2010). When pre-treated by manual scarification, soaking in sulphuric acid or boiling water, germination can reach 90-100% (Razanameharizaka *et al.*, 2006). However, in natural conditions germination is described as "extremely poor", even as low as 0% (De Villiers, 1951). This mismatch between controlled and field results calls for a better understanding of seed fate in the field.

In South Africa, cohorts of baobab trees appear to coincide with good rainfall years and regeneration may only have occurred every 100-150 years (De Villiers, 1951), thus regeneration has been episodic. Venter and Witkowski (2010) reasoned that, as baobabs are long lived trees, reaching at least 1300 years of age (Patrut *et al.*, 2009), populations should survive episodic recruitment even if episodes are separated by many years, even of the order of 100 years. However the environmental context has changed greatly over time as impacts increase within the increasingly human dominated landscapes, particularly in communal lands (Dovie *et al.*, 2005).

The objective of the study was to determine whether recruitment was seed limited or micosite limited and how current land management practices affect future persistence. It was predicted that poor recruitment was due to microsite limitation, a result of inadequate moisture and exposure to livestock, rather than seed limitation.

For seed limitation, the following questions were asked:

1. How much seed do baobab populations produce in a season?
2. What proportion of the seed is viable?
3. Do seeds loose viability over time and can they form persistent soil seed banks?

For microsite limitation, the following questions were asked:

4. What is the natural rate of seedling emergence and in the absence of livestock, what are natural seedling survival rates?
5. To what extent does exposure to livestock (goats and cattle) affect seedling and sapling survival rates?
6. Does survival improve with sapling size (one- and three year old) in the absence and in the presence of livestock?

2. Materials and methods

2.1 Study area

Seed collection and study plots were situated in communally managed land in the Limpopo River valley, commonly known as northern Venda, around 22°50'S and 30°45'E. The study area is bordered by Zimbabwe to the north and the Kruger National Park (KNP) to the east (Fig. 1).

The area lies at an altitude of around 400m above sea level with gently undulating topography and a narrow sandstone ridge running east-west. Soils are derived from sandstone, basalt and aeolian deposits (Venter and Witkowski, 2011a). It is a semi-arid summer rainfall area with a mean annual rainfall of between 334 and 423mm and a high coefficient of variation (CV = 25-40%) (Schulze, 1997). The area is characterized by hot summers (October-March) and mild winters (April-September) with mean monthly maximum and minimum temperatures of 39.7ºC and 8.5ºC for December and July respectively (Mucina and Rutherford, 2006). Frost seldom occurs (Schulze, 1997).

The area falls within the Savanna Biome and more specifically within the Mopane and Lowveld Ecoregions (Mucina and Rutherford, 2006). Baobabs are closely associated with vegetation dominated by *Commiphora*, *Grewia* and *Colophospermum mopane* (Venter and Witkowski, 2011a*)*. Wild fires seldom occur, due to low fuel load. Wildlife is scarce and elephants are now infrequent visitors. In neighboring conservation areas and in rocky outcrops, baboons, which eat the fruit (Venter and Witkowski, 2011b) are common.

Management and ownership of the land and its resources is determined by local customs and structures. Subsistence agriculture and animal husbandry are the main activities (Fig. 2A). The primary management objective is maximization of livestock numbers, thus stocking densities are high and are far above recommended carrying capacities (Dovie *et al.*, 2006).

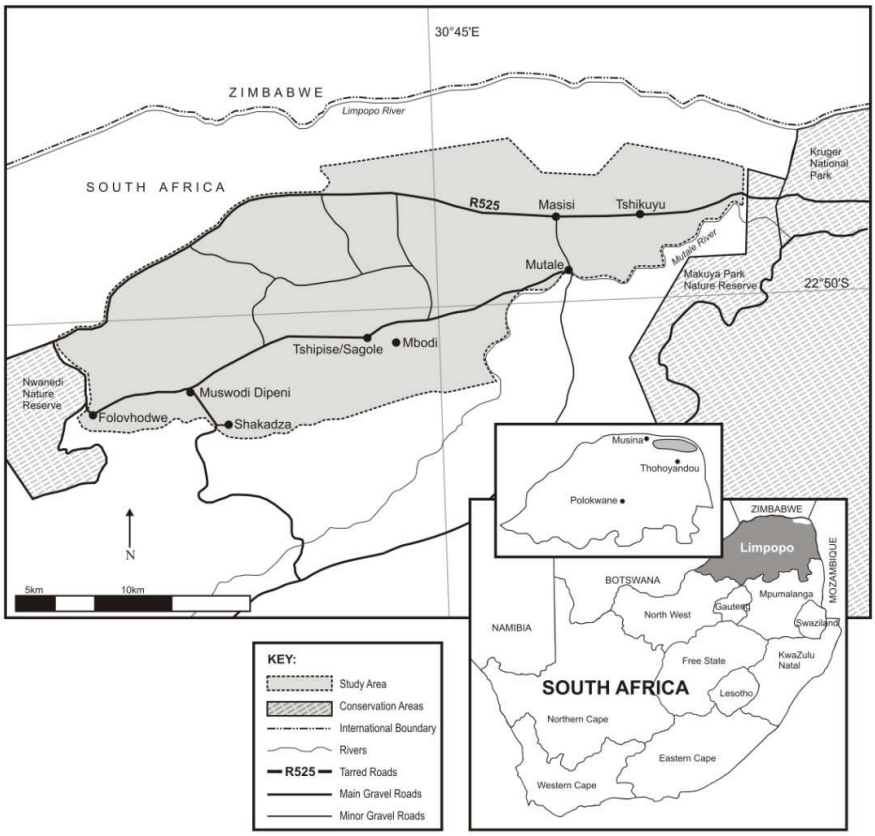

Figure 1. Map of the northern Venda study area indicating where Muswodi Dipeni, Mbodi and Tshikuyu villages (sites of open and closed plots) are situated.

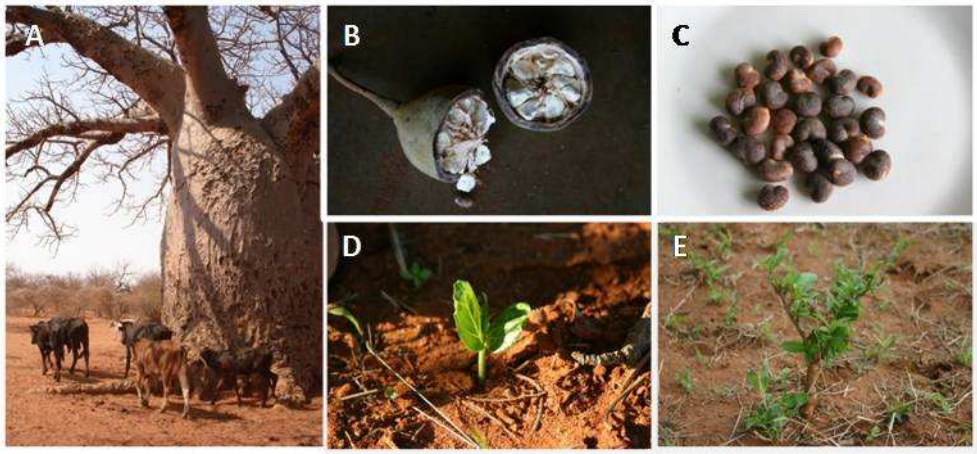

Figure 2. Photographs of livestock in the study area (A), cut baobab fruit showing pulp (B), stored seed (C), newly emerged seedling (D) and sapling (E).

2.2 Study species

Baobabs (*Adansonia digitata)* form part of the family Malvaceae, subfamily Bombacoideacea (Baum, 1995b). Baobab fruit are large, woody, indehiscent capsules (Fig. 2B). Seeds, within the fruit, are imbedded in a whitish powdery pulp (Fig. 2B). The seeds are non-endopermatic, i.e. the dominant embryo includes two cotyledons (dicotylenonous) and a hypocotyl root axis. Germination is hypogeal (Baum, 1995b). Soon after germination, seedlings develop simple leaves (Fig. 2D) and a swollen carrot-like tap root. The tap root functions as a water storage organ until the stem develops water-storage capacity, after which it reduces over time. Once this is developed, usually within the first three months, the young plant is referred to as a 'sapling' (Fig. 2E). Simple leaves may persist for a number of years with 2- and 3- foliate leaves starting to develop as early as the second year in some nursery plants and the typical 5-7- foliate palmate leaves in older plants (Wickens and Lowe, 2008). Saplings shed leaves in winter, which flush again in summer, when plant growth continues. Baobabs are deciduous, bearing leaves and flowers in the wet season (Baum, 1995b).

2.3 Methods

2.3.1 Seed production

Baobab adult tree density and fruit per adult tree was determined for the study area by Venter and Witkowski (2010) and Venter and Witkowski (2011b) respectively. The data was reported for different land-use types (plains, rocky outcrops, fields and villages) and for three fruit sizes (Fig. 3A). Fruit size-classes used were: small (±10 x 5 cm), medium (±15 x

8 cm) and large (±20 x 10 cm), measured as diameter length (stalk to tip) and diameter width (midway between stalk and tip).

In this study, forty five fruit, fifteen from each of the three fruit size-classes (15x3=45) were dissected and the number of seed within each fruit counted to calculate the mean number of seed per fruit size-class.

Venter and Witkowski (2011b) also found that a large proportion of trees in the study area consistently produced less than five fruit a year; these trees were called poor-producers. Therefore only trees that produce more than 5 fruit a year (producers) were included in the calculation.

For each land-use type and each fruit size separately (which were then summed) seed production was determined as follows:

- *Seed/ha = Adult tree density x Proportion producers x Average number of fruit/adult tree x Average number of seed/fruit.*

2.3.2 Amount of viable seed produced

The percentage of viable seed for each of the three fruit sizes, described above, was determined by taking a subsample of 50 seed from each fruit size (n = 50 x 3 = 150 seeds) and determining the viability of each seed with tetrazolium ($C_{19}H_{15}ClN_4$: *M*=334.81 g/mol), using the technique described in MacKay (1972) and Moore (1985). In addition, individual seed mass and fruit pulp (white powder that surrounds the fruit) mass was measured on a digital scale (0.0g precision). Once viability of the seed was determined the predetermined seed mass was allocated to viable and non-viable categories for comparative analysis.

The results of these tests were used to calculate the amount of viable seed produced per ha for each of the communal land-use types and each fruit size separately (which were then summed):

- *Viable seed/ha = Seed/ha x Percentage viable seed.*

2.3.3 Stored and buried seed viability

Over a six year period from 2005 – 2010 baobab fruit were harvested for commercial purposes from the study area. This fruit was cracked open and seed extracted for oil production. Each year a portion of this seed was put aside and stored in sealed plastic bags in dark, cool (±18ºC) conditions (Fig. 2C). The exact tree and specific location, from which any one seed came, was not recorded at the time and therefore could not be allocated to land-use type or fruit-size categories used in 2.3.1.

To determine the proportion of viable seed for each year, a sample of one hundred seeds was drawn from each year's store (2005 – 2009) (n = 5 x 100 = 500 seeds) and viability tested using tetrazolium (as in 2.3.2). The results were compared between years to see if there was any change in viability with seed age. Individual seed mass was measured on a digital scale (0.0g precision) and compared between years. Once it was determined whether the seed was viable or not, the predetermined seed masses were grouped and analyzed for differences in mass.

Persistence in the soil was tested by sowing one hundred cleaned (pulp removed), untreated seed in an enclosed plot in the study area. The plot was cleared of grass and shrubs and enclosed with 12cm diameter chicken mesh, to exclude livestock. Using a hand trowel, small holes (20mm deep) were made in the soil into which the seeds (±5 mm in diameter) were sown. After sowing, holes were filled with the soil. Seeds were planted in a 30 cm x 30 cm grid so that they could be individually located. No further treatment was applied.

The plot was monitored for seedling emergence every two weeks and rainfall recorded daily. Twenty four months later (two years), the remaining seeds were exhumed, counted, weighed and viability assessed using methods described above (2.3.2). The number of viable seeds recovered would indicate the ability of seed to persist in the soil for two years.

2.3.4 Seedling emergence and survival in the absence of livestock (closed plots)

Three 5x10m 'closed' plots (or replicates), enclosed with 12cm diameter chicken mesh, to exclude livestock, were established in the study area. They were located on the edges of three villages (Muswodi Dipeni, Mbodi and Tshikuyu), where they could easily be reached for monitoring purposes (Fig. 1). In late November 2007, at the beginning of the rainy season, 100 fresh untreated seeds (collected in June/July 2007 from within the study area) were sown in each of the three plots (100 x 3 = 300). Seeds were sown in the same manner as described in 2.3.3. No further treatment was applied. Rainfall was recorded daily.

Plots were visited every one to two weeks for 18 months from November 2007 to April 2009 (i.e. over two growing seasons). At each visit, the position of each seed was noted and checked for seedling emergence. Once seedlings had emerged, they were individually monitored to record insect browse (in the form of leaf and stem damage), moisture stress (wilted leaves and stem) and if alive or dead.

2.3.5 Seedling emergence and survival in the presence of livestock (open plots)

Three 5x10m 'open' plots (or replicates), marked with wooden stakes and not enclosed with mesh (so as to allow livestock to pass freely through the plots) were established adjacent to the 'closed' plots described in 2.3.4.

Sowing and monitoring was done in the manner as described in 2.3.3 and 2.3.4. In addition, observations on livestock damage were recorded (as these plots were 'open' as opposed to 'closed'). Evidence of browse (torn leaves and torn stem) and trampling (bent or squashed plants) was recorded and the type of animal (goat or cow) that caused the damage was identified by hoof prints in the soil. Mortality resulting from livestock damage was noted and animal type (goat or cow) and the way in which the seedling died (browsed or trampled) was recorded.

2.3.6 Sapling survival in the absence (closed plot) and presence (open plot) of livestock

Sixty 1-year old and sixty 3-year old saplings were planted in the plots described in 2.3.4 and 2.3.5. Ten 1-yr old plants were planted in each of the three 'open' plots (10x3) and in each of the three 'closed' plots (10x3) next to the sown seeds. Similarly ten 3-yr old plants were planted in each open plot (10x3) and in each closed plot (10x3), next to the 1 year old saplings. Saplings were grown from locally harvested seed and sourced from a nursery within the study area. The local nursery did not keep records on watering regime, but levels of water availability would exceed field levels, however no additional fertilizers were applied. The plants were in good condition when purchased. Planting took place in November 2007, at the beginning of the rainy season and at the same time as seed sowing (2.3.4, 2.3.5). Holes were dug with a pick and spade to about 20cm deep and 15cm in diameter and placed 50 cm apart in rows. Each plant was watered with 2 litres of water at planting, no other treatments were applied.

Plots were visited every one to two weeks for 18 months from November 2007 to April 2009 (i.e. over two growing seasons). At each visit, the following was recorded: plant condition (alive or dead); damage (browsed, trampled); agent of damage (goat, cow, insect) and cause of mortality (browsing, trampling, moisture stress, disease). Browse damage was recorded if leaves had been removed from the stem or if the stem had been severed. Trampling damage was recorded if the stem was bent or the plant was lying horizontal on the ground. Moisture stress was recorded if the plant was wilted. Hoof prints in the soil were used to identify livestock that had caused damage. Herbivory pattern on the leaves helped distinguish between insect and mammalian browsing.

2.4 Data analysis

2.4.1 Seed production

ANOVA followed by Fisher's Least Significant Difference tests (LSD) ($p < 0.001$) was used to test for differences in seed number between small, medium and large sized fruit. To determine the amount of seed produced for the population of baobabs in the study area, the results were used from the formula written in section 2.3.1.

2.4.2 Amount of viable seed produced

The result of viability testing was used in the formula written in 2.3.2 to determine the amount of viable seed produced in the study area. In addition, contingency table χ^2 tested for differences in the proportion of viable seed found between the three fruit sizes. ANOVA followed by Fisher's LSD ($p < 0.001$) and t-tests tested for differences in mass of fruit pulp from different fruit sizes and the mass of viable and non-viable seed respectively.

2.4.3 Stored and buried seed viability

The percentage of viable seed for each of the seed ages was calculated. The number of seed exhumed was given as a percentage of the number of seed that had originally been buried. Similarly the number of viable exhumed seed was given as a percentage of the total number of seed that had been exhumed. Contingency table χ^2, ANOVA followed by Fisher's LSD ($p < 0.001$) and t-tests tested for differences in viability and mass of viable and non-viable seed of different aged seed and seed that had been exhumed.

2.4.4 Seedling emergence and survival in the absence of livestock (closed plots)

For emerging seedlings in closed plots, the percentage of seed that emerged as seedlings and of those, those that survived, were calculated. Days from planting to emergence and days from emergence to death were recorded and mean and SE calculated. Due to very low seedling emergence, the sample size of seedlings was too small to do further statistical analysis or correlations with rainfall. Months in which seedlings emerged and died and causes of death were summarized and presented in a series of figures.

2.4.5 Seedling emergence and survival in the presence of livestock (open plots)

For emerging seedlings in open plots, records and calculations were done as described above (2.4.4).

2.4.6 Sapling survival in the absence (closed plot) and presence (open plot) of livestock

Sapling survival, time to death (months from planting to death) between plots and ages (within plot types) and the interaction between plot and age was compared using χ^2 contingency tables, t-tests and a two-way ANOVA respectively. Cause of death and frequency of damage was calculated for each plant and summarized by age and plot type. Sapling survivorship curves and occurrence and frequency of damage were created for plants of different ages in each plot and overlaid with monthly rainfall.

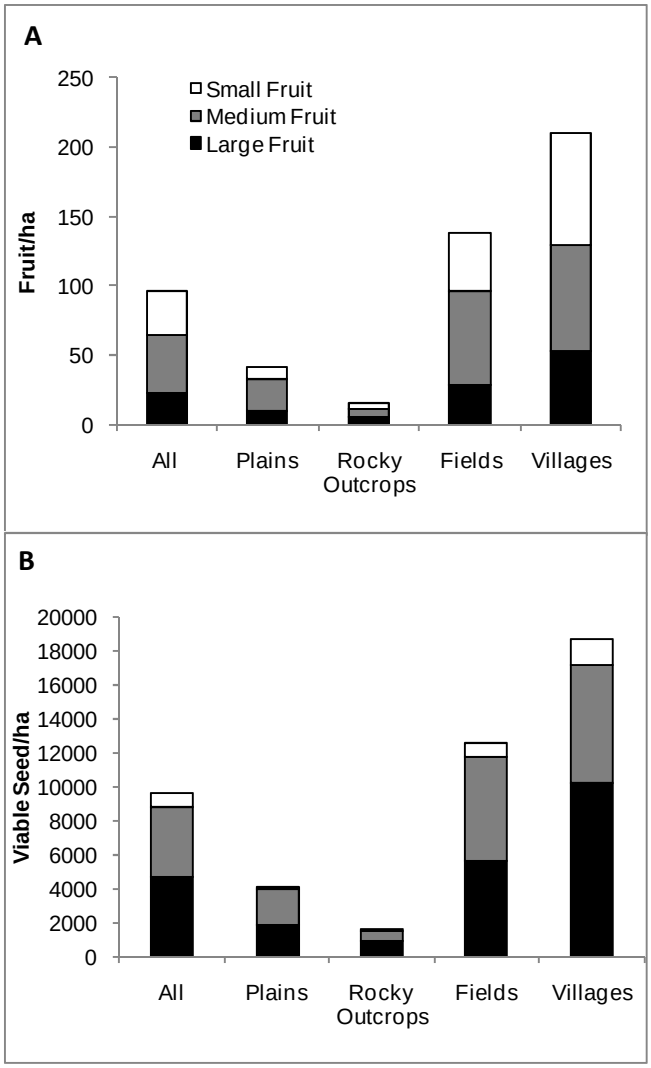

Figure 3. Three year average baobab fruit production (Venter & Witkowski, 2011) (A) and viable seed/ha (B) in communal land-use types.

3. Results

3.1 Seed production

The average annual seed production figure across all land-use types was 5500 ± 2338 seed/ha. Villages and fields had higher densities of baobabs and produced more fruit per tree than plains and rocky outcrops (Venter and Witkowski, 2010, 2011b). Thus viable seed production was considerably higher in villages (11139 seeds/ha) and fields (7458 seeds/ha) compared to plains (2440 seeds/ha) and rocky outcrops (964 seeds/ha) (Fig. 3), the latter site was also impacted by heavy baboon fruit damage. The number of seed/fruit increased significantly with each increase in fruit size ($F_{2,42}$ = 320.75, p < 0.0001) (Table 1).

3.2 Amount of viable seed produced

Proportion of viable seed, mass of viable seed and non-viable seed and mass of fruit pulp increased as fruit size increased (χ^2 = 15.28, df = 2, p < 0.001; $F_{2,133}$ = 105.23, p < 0.0001; t = -4.56, df = 12, p < 0.001; $F_{2,42}$ = 180.16, p < 0.000, respectively) (Table 1). Viable seed was heavier than non-viable seed for both small and medium sized fruit (Table 1).

3.3 Stored and buried seed viability

The proportion of viable seed differed between seed ages (χ^2 = 15.23, df = 5, p < 0.001) (Table 2). Across all seed ages, non-viable seed was significantly lighter than viable seed (Table 2). Non-viable seed mass did not differ between seed ages, but viable seed mass did ($F_{5,32}$ = 1.64, p = 0.1791, $F_{5,606}$ = 35.43, p < 0.0001). The recorded differences in (a) percentage seed viability and (b) seed mass of viable seeds between the fruit crop years (2005-10) may be due to variation in seed source (sizes of fruit or specific area collected from) rather than seed age *per se*.

Thirty four of one hundred seeds (34%) that were sown were exhumed still intact, of which 97% (Table 2) were viable seed, with an additional three seeds having already emerged as seedlings during the trial. The remainder (63%), i.e. seeds that had 'disappeared', could have been (a) eaten, (b) decomposed, (c) germinated and died without emerging above the soil surface or (d) emerged but completely eaten or eaten beyond recognition between monitoring periods. Viable exhumed seed from the persisting seed bank were significantly lighter in mass than viable stored seed of all seed ages ($F_{6,637}$ = 36.32, p < 0.0001) (Table 2).

3.4 Seedling emergence and survival in the absence of livestock (closed plots)

In closed plots, 19 seedlings emerged (6.33%) and of these 1 survived (5.56%). Emergence was staggered over two growing seasons (328± 28 days to emergence) and hence natural germination rates appear to be very slow. Seedlings emergence was limited to December and January (Fig. 4A) and mortality occurred in January, February and March (Fig. 4B). The month of January had the highest seedling emergence and the highest seedling mortality (Fig. 4A, 4B). Most seedlings died within three weeks of emergence (Fig. 4C) with an average time from emergence to death of 21 ± 5 days. Seedlings in closed plots died mostly from moisture stress and some from insect browsing (Fig. 4D). Figure 5 shows weekly rainfall with timing of seedling emergence and mortality and how erratic rainfall, at a critical growing period, may have resulted in moisture stress leading to seedling mortality.

3.5 Seedling emergence and survival in the presence of livestock (open plots)

In open plots, 6 seedlings emerged (2%) and none survived (0%). Emergence took place in November, December and January, 377 ± 5 days after planting (Fig. 4A). All seedlings died of goat browsing within two weeks (Fig. 4C, 4D), with an average time to death of 12 ± 1 days. Figure 5 shows weekly rainfall and timing of seedling emergence and mortality.

3.6 Sapling survival in the absence (closed plot) and presence (open plot) of livestock

3.6.1 The effect of livestock on sapling survival

Results show that saplings that are protected from livestock have a better chance of survival than those exposed to livestock. Sapling survival in closed plots (65%) was significantly higher than in open plots (10%) (χ^2 = 38.72, df = 1, $p < 0.0001$) and 'average time to death' of saplings in closed plots was significantly longer (10.45 ± 0.97 months) than in open plots (4.33 ± 0.45 months) (t = -6.47, df = 73, $p < 0.0001$). The results from a two-way ANOVA indicated that there was no significant interaction between open and closed plots and sapling age in 'time to death' ($F_{1,73}$ = 0.18, p = 0.6725).

3.6.2 One- and three year old sapling survival in closed plots (livestock excluded)

In closed plots the survival of three-year old saplings (87%) was significantly greater than one-year old saplings (47%) (χ^2= 47.73, df = 1, $p<0.0001$). Time to death of three-year old saplings tended to be longer (12.2 ± 0.49 months) than one-year old saplings (9.9 ± 1.24 months). Figure 8 indicates that in closed plots moisture stress, soon after planting and just

before the rains, was the main cause of mortality of both one- and three-year old saplings (Fig. 6). In Mbodi village stems dried out and withered back so that the underground tuber was the only part of the plant which remained alive during winter. In Tshikuyu many stems managed to survive above ground during winter, but developed a black-coloured disease (samples have been sent to a plant pathology laboratory for identification). Although 13% of deaths are attributed to disease, not all diseased plants died. Insect browsing increased during the rains in response to leaf growth, and was responsible for more deaths (31%) than disease (Fig. 6).

3.6.3 One- and three year old sapling survival in open plots (livestock present)

In open plots, survival of three-year old saplings (13%) was significantly better than one-year old saplings (7%) (χ^2 = 31.48, df = 1, p<0.0001). Repeated livestock browsing and trampling was responsible for 86% and 100% of deaths of one- and three-year old saplings respectively, while moisture stress accounted for the remaining 14% of deaths of one-year old saplings (Fig. 6). Time to death of three-year old saplings tended to be longer (5.06 ± 0.61 months) than one-year old saplings (3.66 ± 0.65 months) (Table 3).

Figure 7 indicates that browsing by goats occurred mostly in the first year and soon after planting. After being browsed, plants flushed more leaves and were then browsed again. Many plants died after the second browsing event, probably due to depletion of stored reserves. During the dry season, plants lack leaves, so browsing seldom occurs. Browsing did not coincide with rainfall in the second year because the plants were so badly trampled that they barely showed above the ground. Trampling took place throughout the year regardless of whether plants had leaves or not. Trampling was more frequent in Tshikuyu village because a cattle path developed through the plot. Trampling often broke the stem and saplings regenerated (resprouted) from their underground tuber.

Saplings were more susceptible to goat browsing than trampling and died more quickly when only browsed than when only trampled (Table 3). Three-year old saplings appeared to be less resilient to the combination of browsing and trampling than one-year old saplings. Saplings that survived were only browsed once and managed to survive repeated trampling events (Table 3).

Table 1. For each fruit-size category the following is given: number of fruit dissected (N), pulp mass (mean ± SE), seed number/fruit (mean ± SE), percentage viable seed, viable seed mass (mean ± SE), number of viable seed (n) which was also used to determine the mean and standard error of the viable seed mass, non-viable seed mass (mean ± SE), number of non-viable seed (n) which was also used to determine the mean and standard error of the non-viable seed mass. Large fruit did not have any non-viable seed, hence no *n* in the second last column. T-test compares viable and non viable seed mass.

Fruit size category	N	Pulp mass (g)	Seed/fruit	*Viable seed (%)	Viable seed mass (g)	n	Non-viable seed mass (g)	n	t -test t
Small Fruit	15	2.53 ± 0.07^{A}	24.40 ± 1.23^{A}	78	0.41 ± 0.01^{Ab}	39	0.22 ± 0.02^{Aa}	11	10.8847
Medium Fruit	15	11.87 ± 0.2^{B}	96.93 ± 4.25^{B}	94	0.61 ± 0.01^{Cb}	47	0.43 ± 0.03^{Ba}	3	6.5407
Large Fruit	15	23.47 ± 1.33^{C}	194.47 ± 6.96^{C}	100	0.54 ± 0.01^{B}	50	-		-

A,B,C indicate significant differences within each column and a,b within rows ($p<0.05$)
t-test results are between viable and non-viable seed within fruit sizes (a,b)
* % viable seed based on a sample of 50 seeds from each fruit size.

Table 2. Percentage of viable seed and mass of viable and non-viable fresh, stored (all from harvested fruit) and persistent seed bank seeds. T-test compares viable and non-viable seed mass.

Source of seeds (seed age: years)	Viable Seed (%)	Viable seed mass (g)		Non-viable seed mass (g)		t-tests	
		Mean ± SE	n	Mean ± SE	n	t	*p*
Fruit 2010 (fresh)	91	0.54 ± 0.01^{Cb}	136	0.26 ± 0.03^{Aa}	14	10.8934	<0.001
Fruit 2009 (1 year old)	94	0.48 ± 0.01^{Bb}	94	0.32 ± 0.03^{Aa}	6	4.7411	<0.001
Fruit 2008 (2 years old)	89	0.60 ± 0.01^{Eb}	89	0.35 ± 0.03^{Aa}	11	9.2953	<0.001
Fruit 2007 (3 years old)	99	0.47 ± 0.01^{B}	99	0.50^{A}	1	-	-
Fruit 2006 (4 years old)	98	0.56 ± 0.01^{Db}	98	0.30 ± 0.00^{Aa}	2	3.3991	<0.001
Fruit 2005 (5 years old)	96	0.47 ± 0.01^{Bb}	96	0.32 ± 0.20^{Aa}	4	2.7470	0.007
Seed bank seed (2 years)	97	0.42 ± 0.01^{A}	33	0.40^{A}	1	-	-

A,B,C indicate significant differences within each column ($p < 0.05$) and a,b within rows.

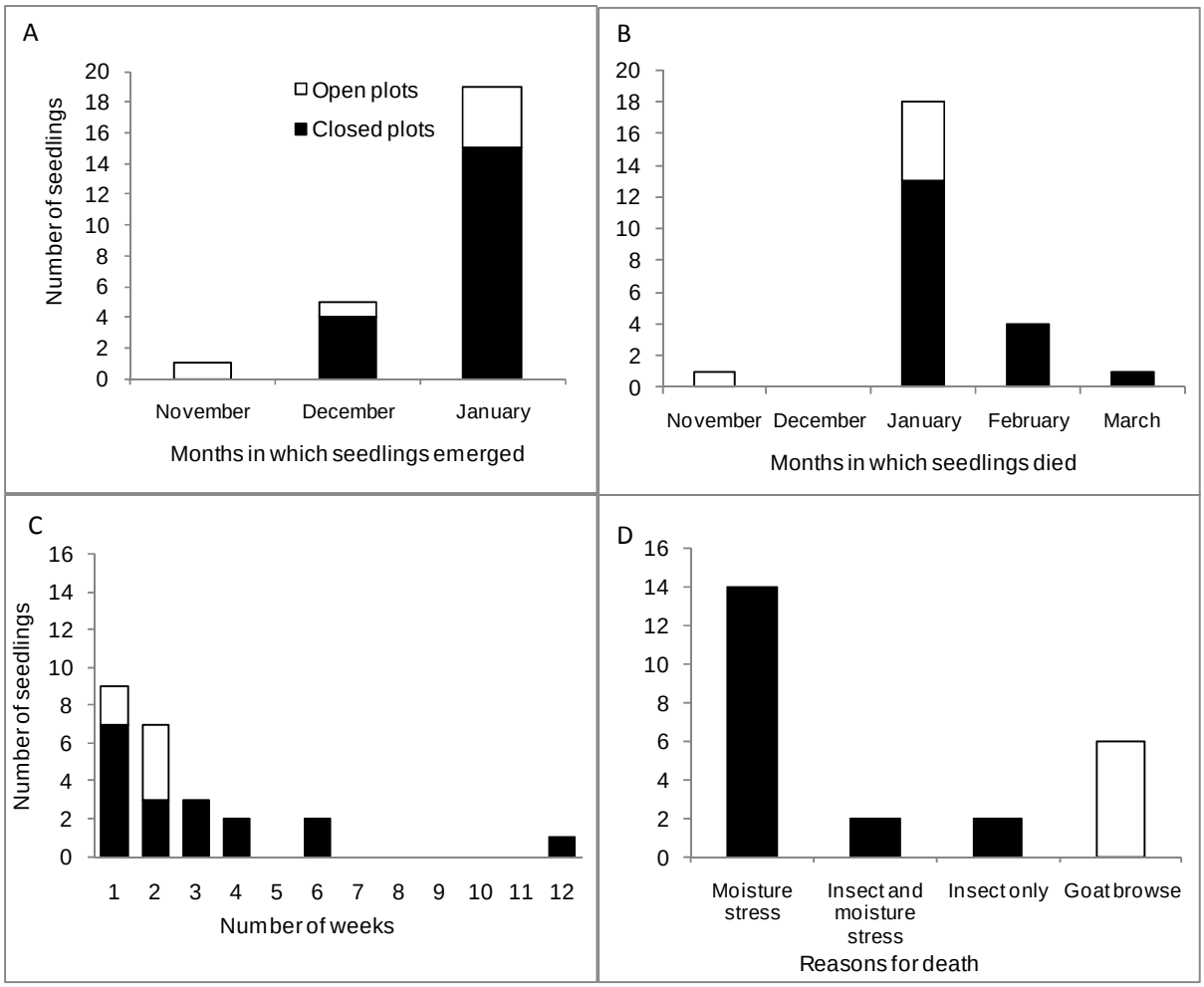

Figure 4. Months in which seedlings emerged (A) and died (B), weeks to death (C) and reasons for death (D) in open (white bars) and closed (protected from livestock damage) (black bars) plots.

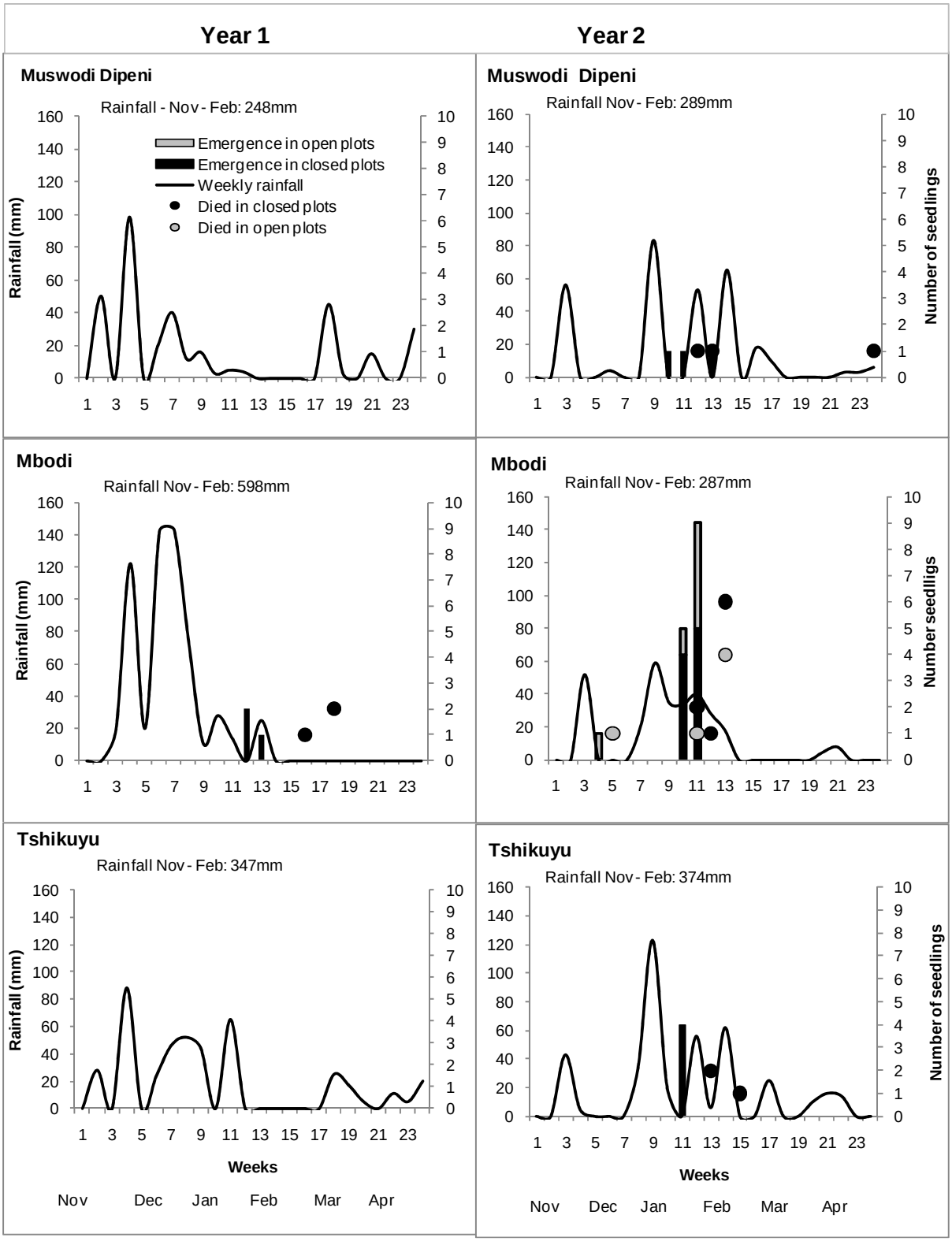

Figure 5. Weekly rainfall, seedling emergence (bars) and seedling mortality (circles) for closed (black fill) and open plots (grey fill) for 24 weeks over two summer seasons (Year 1: November 2007 to April 2008 and Year 2: November 2008 - April 2009) at three sites: Muswodi Dipeni, Mbodi and Tshikuyu villages, Venda, South Africa. No seedlings emerged (or died) at Muswodi Dipeni and Tshikuyu in Year 1. Left y-axis indicates rainfall and right Y-axis indicates all remaining variables.

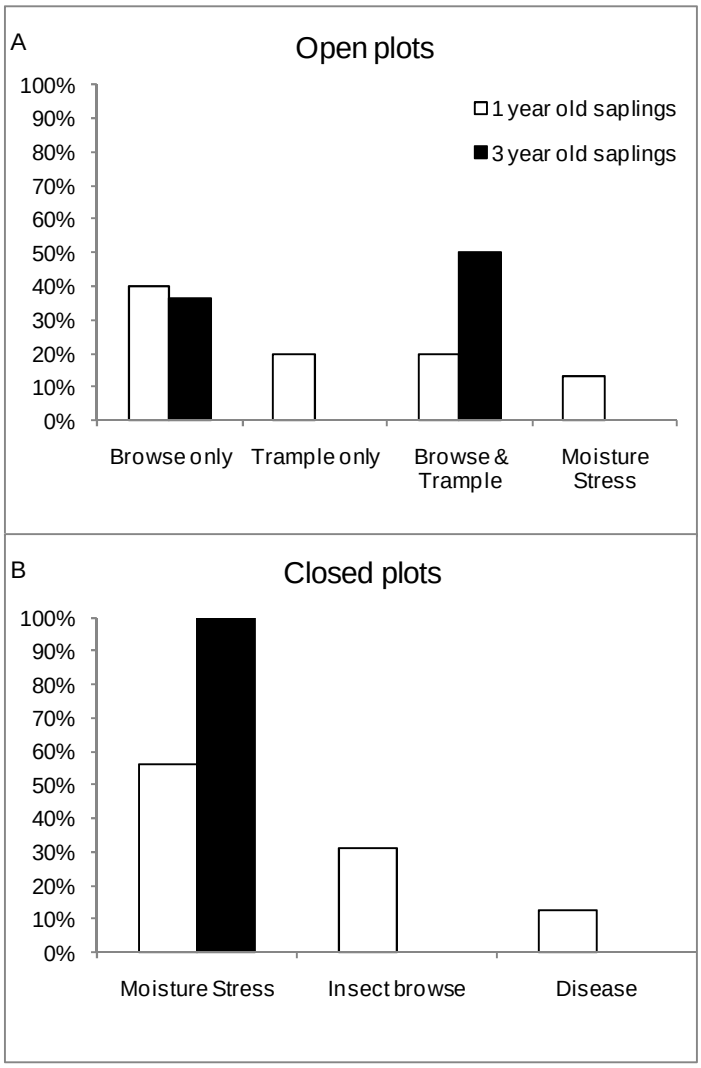

Figure 6. Cause of damage and mortality in open (A) and closed (B) plots for one- (white bars) and three-year old (black bars) baobab saplings.

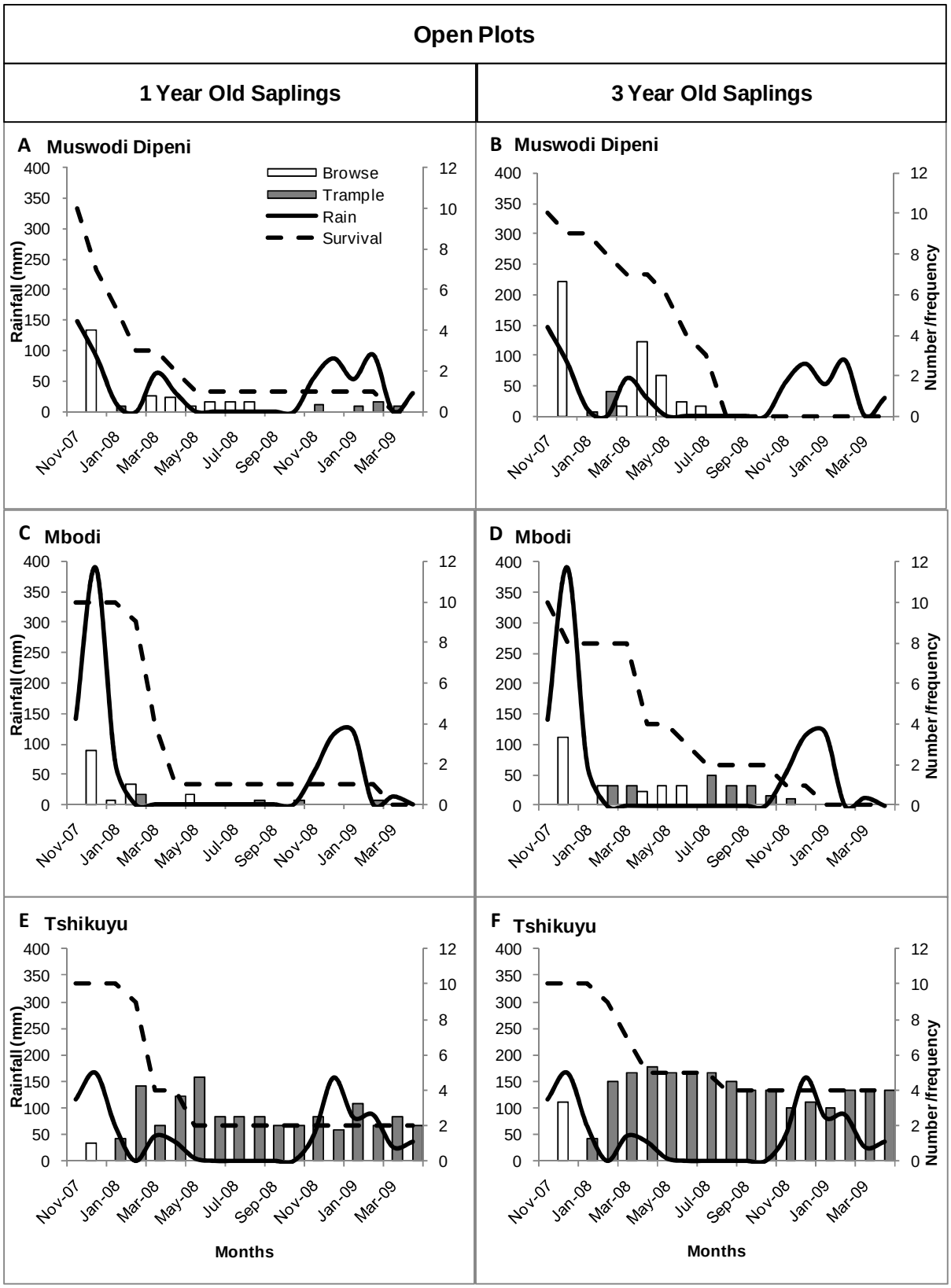

Figure 7. Monthly rainfall (solid line) and survivorship (dashed line) curves, occurrence (timing) and frequency (number of plants affected per month) from browsing (white bars) and trampling (grey bars) during the period November 2007 to April 2009, for one- (A,C,E) and three-year old (B,D,F) baobab saplings in open plots at Muswodi Dipeni (A,B), Mbodi (C,D) and Tshikuyu (E,F) villages, Venda, South Africa. Left y-axis indicates rainfall and right Y-axis indicates all remaining variables.

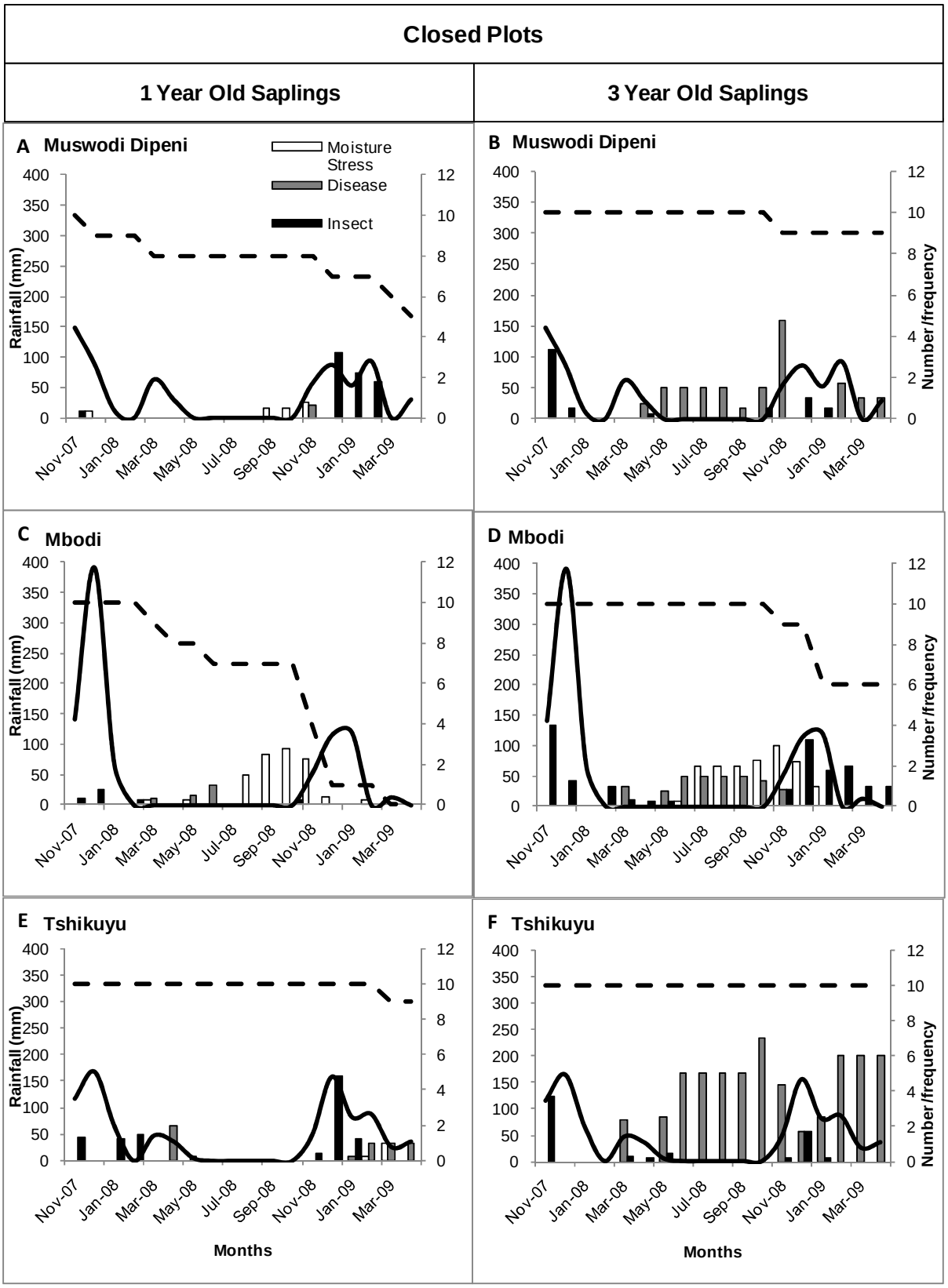

Figure 8. Monthly rainfall (solid line) and survivorship (dashed line) curves, occurrence (timing) and frequency (number of plants affected per month) from moisture stress (white bars), disease (grey bars) and insect browsing (black bars) during the period November 2007 to April 2009 for one- (A,C,E) and three-year old (B,D,F) baobab saplings in closed plots at Muswodi Dipeni (A,B), Mbodi (C,D) and Tshikuyu (E,F) villages, Venda, South Africa. Left y-axis indicates rainfall and right Y-axis indicates all remaining variables.

Table 3. The number of one- and three-year old baobab saplings in open plots that were browsed and trampled (first column), average number of times damage was recorded (second column) and time to death (third column). Browsing was caused by goats and trampling by cows.

	1 - year old				3 - year old			
	Number of plants	Browse (mean±SE)	Trample (mean±SE)	Time to death (months)	Number of plants	Browse (mean±SE)	Trample (mean±SE)	Time to death (months)
Damage to plants that survived								
Browsing only	0	-	-		0	-	-	
Trampling only	1	-	32.0±0.0		0	-	-	
Browsing & trampling	1	1.0±0.0	35.0±0.0		4	1.0±0.0	39.3±3.66	
Total survival	**2 (7%)**				**4 (13%)**			
Damage to plants that died								
Browsing only	12	2.13±0.33	-	2.50±0.43	11	4.0±0.81	-	4.41±0.92
Trampling only	6	-	8.0±4.64	3.17±0.40	0	-	-	
Browsing & trampling	6	2.3±0.98	9.8±5.28	7.50±2.39	15	2.0±0.39	4.1±1.17	5.53±0.82
Moisture stress	4			2.13±0.72	0	-	-	
Total mortality	**28 (93%)**				**26 (87%)**			
Average				**3.66±0.65**				**5.06±0.61**

4. Discussion

The total number of available seed is determined by a species' adult abundance and fecundity (Muller-Landau *et al.*, 2002). Baobab fruit production is highly variable in space (Assogbadjo *et al.*, 2005) and time (CV = 44.7 over three years (Venter and Witkowski, 2011b)). Furthermore, this study has shown that baobabs in human-modified areas (villages and fields) produce more seed than in more natural areas (plains and rocky outcrops). In human-modified areas, higher adult tree density and higher fruit production, possibly aided by sparse ground cover and dripping water taps, result in substantial seed production in the order of 10^4 seeds/ha per annum. However in natural landscapes both lower tree density and lower fruit production/tree result in lower seed production, in the order of about 10^3 seeds/ha per annum, but still deemed high enough not to be an attributing factor to poor recruitment. However, in natural areas, where baboons occur, predation of baobab fruit could be a major contributing factor to poor recruitment. When mature fruit is eaten the seeds are not destroyed and baboons act as useful seed dispersers, but when immature fruit is eaten the developing seed is destroyed (Pochron, 2005). Baboons are known to reduce fruit production by at least 85% on the ridges and within nature reserves in the study region (Venter and Witkowski, 2011b). Furthermore, unpublished data from Skelmwater (long term growth monitoring plot near Musina, South Africa) show that predation of baobab fruit by baboons has resulted in multiple crop failures. Fruit predation may also be a contributing factor to poor recruitment in the Kruger National Park (KNP) and Mana Pools National Park,

Zimbabwe, where an absence of saplings has been noted (Swanepoel, 1993; Hofmeyr, 2003). No other fruit predator (other than baboons) has been found in ongoing (2007 - 2011) fruit production surveys. Once fruit mature they drop off the trees and are mostly collected by the villagers and a few by baboons, thus the main dispersal agents are people who live in the area (SM Venter, unpublished data).

Seed viability is a crucial component to assessing seed availability. Results from germination experiments in other parts of Africa suggest that across its distribution range baobab trees produce a high proportion of viable seed (over 90%) (Esenowo, 1991; Danthu *et al.*, 1995; Razanameharizaka *et al.*, 2006). It is known that baobab seeds are able to survive for many years under laboratory conditions, e.g. at 8% moisture and 5ºC, seeds still had a 94% germination success after fifteen years (Wickens and Lowe, 2008). Similarly, in this study, all seeds remained intact (100%) and had high viability ($\geq$89%) when stored under 'controlled conditions' (ambient room temperature). Although the seed exhumed from the field had similar high (97%) viabilities, only 34% of the original batch was still intact after two years (Section 3.3). Nonetheless, the availability of viable seeds does not appear to be a significant factor that would limit recruitment. However, more detailed studies on the fate of seed in soil seed banks would be useful.

Other semi-arid savanna woody plants such as *Acacia* spp., *Dichrostachys cinerea* (Witkowski and Garner 2000) and *Burkea africana* (Wilson and Witkowski 2003), all having seeds with hard seed coats, have been shown to form persistent seed banks. It is known that seeds of some African *Acacia* spp. are able to survive extreme soil surface temperatures ranging from 50 - 70ºC for at least a month (Mbalo and Witkowski, 1997; Witkowski and Garner, 2000) but more deeply buried seeds, which have a much more ameliorated temperature range, persist for longer (ETF Witkowski unpublished data). As baobab seeds have a hard impermeable seed coat they are also protected, to a certain extent, from pathogens and predators, and this study has shown that they also form persistent seed banks with 34% of seeds persisting for at least two years. Ninety seven percent of the recovered seeds that were buried for 24 months were still viable, but 63% of seeds that had been buried had disappeared. Some of these seeds may have germinated and then died (Wilson and Witkowski, 1998) or may have been predated (Helm *et al.*, 2011) over the 24 month period. However, substantial seed production, high seed viability and 34% of seeds persisting in a soil seed bank after 24 months of burial, suggests that, at least in areas were baboons do not occur, recruitment is not seed limited.

Seeds with an impermeable seed coat will spread germination over a number of years allowing for long-lived seed reserves with germination taking place at the same time each year (Geldenhuys, 1993; Baskin and Baskin, 2001). We found that most seedlings

emerged in January, either in the first or second year (Fig. 5). Hofmeyr (2003) noted that baobab seeds staggered their germination over at least three years in nursery conditions in the KNP adjacent to the study region. High fluctuating temperatures are typically required to overcome dormancy in Malvaceae (Baskin and Baskin, 2001). In Southern Africa temperatures start increasing in October and remain high through to April (South African Weather Service). January is the wettest and hottest month of the year and exhibits the lowest diurnal temperature variation which may provide the cue for the observed peak germination in January.

In South Africa, it has been estimated that effective baobab regeneration may only occur every 100–150 years (De Villiers, 1951), i.e. episodic regeneration. Jagged size-class distributions (Venter and Witkowski, 2010) could be seen to mirror paleo-climatic conditions (Huffman, 2010) that may represent poor recruitment during dry periods. By studying rainfall records and young baobabs in the field, De Villiers (1951) suggested that the then current crop of juveniles might have recruited in 1909, 1918 and 1923. The lack of juveniles below 50cm dbh in 2006 (Venter and Witkowski, 2010) suggests successful recruitment may not have occurred since 1923.

This study confirmed that seedling establishment is severely hampered by poor and inconsistent rainfall. Over 18 months of observation the majority of seedlings in closed plots survived only three weeks and only one seedling survived the entire period. Poor rainfall is given as the reason for poor baobab seedling survival in many other regions (De Villiers, 1951; Dhillion and Gustad, 2004; Chirwa *et al.*, 2006), but it is more likely that seedling mortality is a result of inconsistent intra-seasonal rainfall rather than low rainfall *per se*. It has been shown with other semi-arid African savanna species, that seedlings need frequent, and not necessarily high rainfall to survive initially (Wilson and Witkowski, 1998). The results of this study show that seedling emergence can occur in years even when early season rainfall is as low as 287 mm (Mbodi: [July-June] 2008/2009) and that in the year that received 589 mm (Mbodi: 2007/2008), seedlings emerged but were unable to survive due to erratic post-emergence rainfall. Rainfall in this area is very seasonal with first rains (>50mm) in November and last rains (>50mm) in April. Baobabs have a limited growing season with leaf flush adhering closely to these months (S.M. Venter, unpublished data). Thus it may be important that germination occurs relatively early in the season so that the young plants have enough time to acquire resources to survive the winter, yet inconsistent rainfall and predation hamper survival, hence resulting in episodic recruitment.

Livestock is often mentioned as a threat to baobab recruitment (Romero *et al.*, 2001; Dhillion and Gustad, 2004; Chirwa *et al.*, 2006). Many plants survive herbivory by resprouting (Bond and Midgley, 2001; Helm *et al*., 2009) and this appears to be a strategy for young baobabs. Soon after germination and within the first few months of growth,

baobabs develop an underground tuber in order to support regrowth after browsing or damage (Wickens, 1982; Bond and Midgley, 2001). Dhillion and Gustad (2004) found that once a seedling had established, persistent browsing hampered growth, but did not kill plants. Goats and sheep are associated with poor tree cover in African savannas whereas cattle (as obligate grazers) are not (Groen *et al.*, 2011). Our results show that saplings died more quickly after goat browsing than cattle trampling, but that after repeated damage, of either browsing or trampling, their reserves were too depleted to survive. In conservation areas, goats and cattle are replaced by a variety of wild herbivores such as impala, kudu, eland, zebra and buffalo. Baobab recruitment in conservation areas, such as the KNP, may be hampered by the presence of ungulate browsers and grazers, for similar reasons that marula declined in the KNP (Helm *et al.*, 2009).

The study region has a low fire frequency (MacGregor and O'Conner, 2002), so unlike moister areas where fire can greatly impede seedling establishment, fire is unlikely to be a major impediment, although it may reduce the frequency of episodic recruitment events, when moisture levels are sufficiently high that fuel loads can carry a fire.

Baobabs are extremely sensitive to frost, which can cause baobab seedling mortality (Sidibe & Williams, 2002). Thus, in areas where frost does occur the frequency and intensity of frost should be considered. However, where baobabs occur in southern Africa, frost is limited to 0-5 days of the year and in the study area specifically, frost never occurs (Schulze, 1997).

To enhance recruitment, active planting and protection of young seedlings may be required. In West Africa a higher density of baobab seedlings and young trees were found in villages than in surrounding fallows. This was attributed to seed being dispersed in village garbage and the care local people take of baobab seedlings and saplings (Dhillion and Gustad, 2004; Assogbadjo *et al.*, 2005; Duvall, 2007). Interviews conducted in Mali by Dhillion and Gustad (2004) found that 50% of respondents protect naturally germinated seedlings and 60% had transplanted seedlings for protection. Villagers built barriers to prevent browsing, irrigated seedlings, prepared basin-shaped beds for water collection around seedlings and pruned and cut back surrounding vegetation. These protective actions are motivated by the high value people in West Africa place on baobab products (leaves, fruit, bark) and their cultural significance. Baobab leaves are a staple crop in Mali and surrounding areas so the tree, as a food source, is very important. In South Africa, local people tend not to protect young plants even though there are two sets of National legislation that protect baobabs, the National Environmental Management and the National Forest Act (Department of Water Affairs and Forestry, 1998; Department of Environment Affairs and Tourism, 2004). This legislation is poorly enforced and unless local people

develop a ‘baobab culture’, as is seen in West Africa, recruitment constraints are likely to hamper future populations.

5. Conclusion

The results of this study clearly indicate that baobab recruitment is microsite limited and not seed limited. The baobab population in the study area is able to produce large quantities of viable seed. Viability tests on stored and exhumed seed indicate that persistent seed banks are formed and can be maintained by annual seed input and staggered germination (mainly in January each year), with each seed crop germinating over a number of years. Thus recruitment is not limited by seed availability.

Baobab recruitment is shown to be severely hampered by microsite conditions. This study showed that poor regeneration is influenced by the lack of consistent rainfall required to support seedling survival. This situation is exacerbated by livestock browsing and trampling, resulting in extremely high rates of seedling and sapling mortality.

Baobab populations could possibly be maintained with low episodic recruitment (Venter and Witkowski, 2010), but if conditions for recruitment do not re-occur, then there may be cause for concern. Climate change models predict that many areas where baobabs occur will get dryer and hotter (Cuni Sanchez *et al.*, 2011). This, in addition to rapidly increasing human and livestock populations, implies that future recruitment events may be even more hampered. A viable adaptation to this long term change is active planting, protection and monitoring of young plants, in order to maintain baobab populations in these landscapes.

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Chapter 7

Submitted paper

Fruits of our labour: contribution of commercial baobab (*Adansonia digitata* L.) fruit harvesting to the livelihoods of marginalized people in southern Africa

Abstract

Baobabs (*Adansonia digitata*) provide products, mainly bark, leaves and fruit, which are used for subsistence purposes and traded to generate cash. Recently, demands for baobab fruit derivatives on the global market, namely pulp and seed oil, have increased rapidly, leading to concerns over the negative impacts on subsistence users. This study focussed on the value of baobab fruit in Limpopo Province, South Africa. Baobab fruit had a higher income value (4x) than direct-use (subsistence) value and contributed to 38% and 4% respectively to overall value of non-timber forest products. Cash earned was used to buy food (73%) and invest in small businesses, indicating a move from subsistence to cash economy. It is suggested that commercialization of baobab fruit will have far-reaching benefits; and that secured access to trees and investment in local beneficiation will further increase the value of the resource for many marginalized people in southern Africa.

Key words

Direct-use value; non-timber forest products (NTFP); subsistence use; women; Venda

1. Introduction

Many marginalized and poor communities around the world rely on non-timber forest products (NTFPs) for their survival (Shackleton and Gumbo 2010). NTFPs refer to any wild biological resource harvested by rural households for domestic consumption or trade (Shackleton *et al.* 2007). NTFPs are important for health, food, nutrition, religion, shelter and energy and through their economic contribution provide a safety-net when other sources of income fail to meet household needs (Dovie *et al.* 2002; Shackleton *et al.* 2002).

Rural livelihoods are often supported by diverse income streams. These include, among others, income from employment, grants, trade and NTFPs. The income contribution of NTFPs includes cash derived from sales of these products and their value through direct- or subsistence use. Valuation techniques create a monetary value for direct-use products which allow comparisons to be made between income streams (Clarke and Grundy 2004). In this way the contribution of NTFPs to total livelihood can be evaluated (Dovie *et al.* 2002). The cash value and direct-use value of NTFPs to rural households has been calculated to be worth several hundred dollars per annum (Dovie *et al.* 2005; Shackleton and Gumbo 2010).

Increasingly, rural dwellers are selling products that were previously used for subsistence purposes (Dovie *et al.* 2005). This change is driven at a local level by a greater

need for cash as people become more integrated into a market economy and face economic hardship and unemployment (Belcher *et al.* 2005). Generally, returns from the sale of NTFPs are modest, but the low entry barriers to trade means that they provide an important option for poor and marginalized people with minimal education and skills (Shackleton and Gumbo 2010).

Baobabs (*Adansonia digitata*) provide a number of NTFPs that are used for subsistence and are also sold to generate income. All parts of the plant are used, with over 300 uses of baobab products recorded (Buchmann *et al.* 2010). In particular, the composition and nutritional value of the bark, leaves, fruit pulp and seeds make it an important tree for subsistence as well as commercial use (Gruenwald and Galizia 2005; Chadare *et al.* 2009). The bark is high in fibre and is used for making ropes and weaving while the leaves are eaten as spinach or used in relishes. The fruit contains two distinct products, the seed and the surrounding pulp. The seed is pressed to yield oil used in cosmetic formulations while traditionally it is eaten roasted and pounded. The tart fruit pulp, a dry powder that surrounds the seed, is also used as a food ingredient (Sidibe and Williams 2002).

In southern Africa baobab fruit are considered to be relatively underutilized, and by commercializing this resource a significant contribution could be made to alleviating poverty in rural areas (Gruenwald and Galizia 2005). Over the last decade, locally-based companies have started to buy the seed and fruit of a number of tree species from rural communities in Botswana, Malawi, Mozambique Namibia, South Africa and Zimbabwe. The demand for baobab fruit is driven by cosmetics and food companies, locally and internationally lobbying to increase the value and market share of its products, and to get better returns for producers, which has taken many years (Welford and Le Breton 2008). Baobab oil has been sold in European and US markets for some time: in 2008 the European Union approved baobab fruit pulp as a novel food ingredient (Vassiliou 2008), and in 2009, the Food and Drug Administration in the United States of America (USA), gave approval for importation (Tarantino 2009).

Despite the potential benefits associated with the commercialization of baobab products, it is feared that this commercialization of the resource on the global market may have serious consequences on the subsistence use of baobab products, particularly in West Africa where there is heavy dependence on leaves and fruit for daily nutrition and income (Buchmann *et al.* 2010). There is thus a need to also determine its value (income and subsistence) and to describe positive and negative effects of commercialization of the fruit on local people. This study evaluates the direct use-value (subsistence) and cash-value of baobab fruit in a rural community in South Africa, and compares this to other income streams received by harvesters. It describes the socio-economic background of the

harvesters involved in collecting baobab fruit and their perceptions of the ecology and management of the resource. Based on these findings, the implications of commercializing baobab fruit are discussed and recommendations regarding sustainable and equitable commercialization are made. In this study the following key questions were posed:

1. Who are the baobab harvesters in terms of gender, age and education relative to the rest of the population in the area?
2. What is the cash value of income from baobab fruit compared with other NTFPs and how does this compare to income from social grants and employment?
3. What is the direct use-value of baobab fruit compared with other NTFPs?
4. What are the implications of the commercialization of baobab fruit?
5. What are the harvesters' perceptions regarding the ecology, use and management of baobab trees?

2. Materials and methods

2.1 Study area

The study area falls in the Mutale District Municipality, also known as northern Venda, a remote rural area of Limpopo Province. Limpopo Province is one of the poorest provinces in South Africa (Limpopo-Provincial-Government 2009). The area centres on 22°50'S and 30°45'E, with Zimbabwe to the north, Botswana to the west and the Kruger National Park (KNP) to the east (Fig. 1). The area falls within the Savanna Biome and more specifically within the Mopane and Lowveld Ecoregions (Mucina and Rutherford 2006).

The population in Mutale District Municipality is just over 100 000 people, of which 59% are women. Of these, 86% are unemployed and 6% receive state pensions (Fig. 2). Education levels are low, with 33% of women and 14% of men having never been to school (Statistics-S.A. 2001). The study area is semi-arid, receiving from 334-423 mm annual rainfall with a high coefficient of variation (CV=25-40%) (Schulze 1997), thus attempts at subsistence agriculture result in very inconsistent and at best low yields. Furthermore, livestock overstocking has led to widespread overgrazing and general degradation of the environment (pers. obs). There are few industries in the area, thus job opportunities are extremely limited.

The people of this region are part of the BaVenda ethnic group (Stayt 1931). The region comprises a series of villages, each with its own traditional leader, who form part of a larger traditional hierarchy with democratically-elected representatives known as 'civics' sharing leadership responsibilities. There are no banks or national supermarket chains in

the area and ‘spazas’ or ‘supas’ are the small local shops and stores where groceries and implements are purchased. Informal saving and credit associations, such as burial societies known locally as ‘stokvels’, are a means of facilitating savings amongst women (Bouman 1995). The South African government pays ‘pensions’ to people of >60 years and ‘child grants’ to the guardians of children <16 years. These are non-contributory grants to unemployed South Africans, who qualify for pensions on the basis of age or for child grants if they have young children.

Initiated by a locally based company, the commercial harvesting of baobab fruit began in 2006 and by 2010 over 1500 harvesters where involved. Cleaned seed was collected and cold-pressed with a screw press to extract the seed oil. The oil was sold as an ingredient to the cosmetics market in South Africa, Europe and the USA.

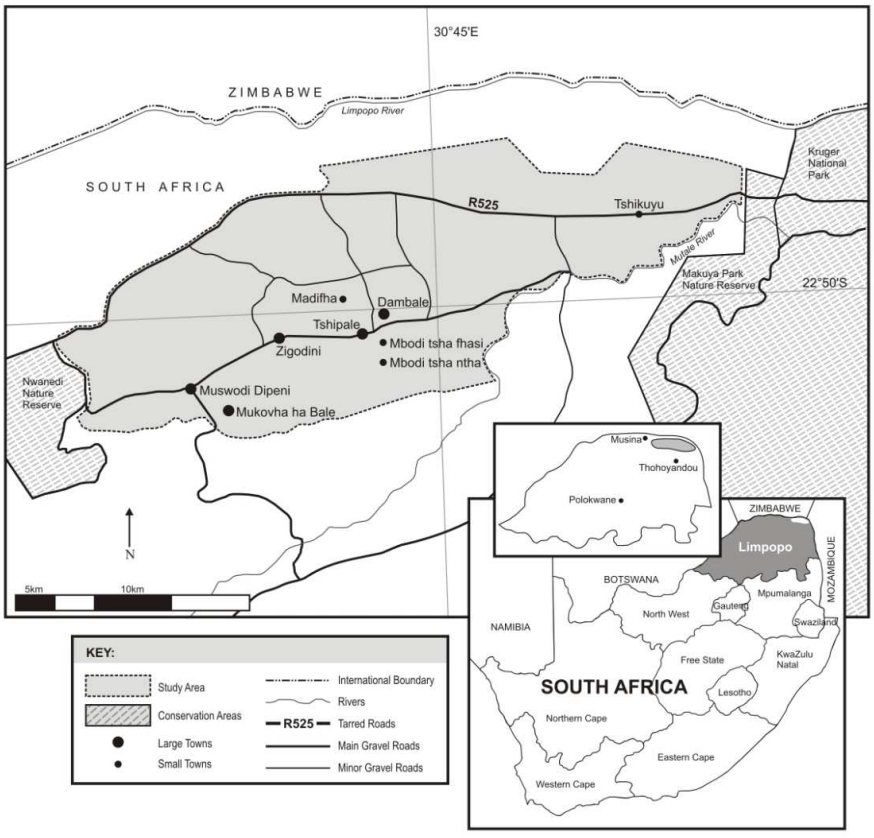

Figure 1. Map indicating location of villages in the study area.

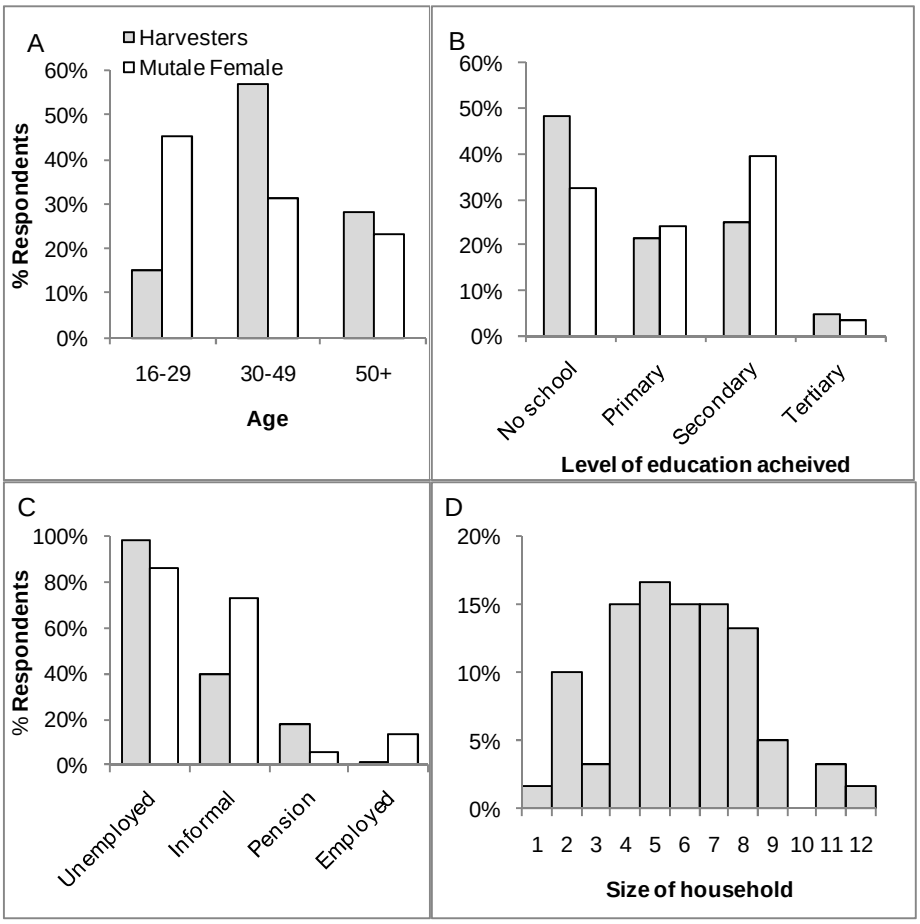

Figure 2. Percentage of respondents (n=60) and females in the Mutale municipal area of different age classes (A), levels of education (B) and income streams (C), plus the percentage of respondents with household sizes that range from 1 - 12 people (D).

2.2 Study species

Baobabs (*Adansonia digitata* L.; Malvaceae, subfamily Bombacoideacea) occur widely across Africa and are found in most countries south of the Sahara (Sidibe and Williams 2002). Baobabs are associated with savannah vegetation and have a wide tolerance to variations in rainfall, temperature and altitude, but are generally found in drier, low-altitude plant communities receiving between 200-800 mm of rainfall annually (Wickens 1982). The population density of baobabs in the study area varies between land-use types, with human-modified landscapes having higher baobab tree densities (1.65 ± 0.36 plants/ha) than natural landscapes (0.90 ± 0.17 plants/ha) (Venter and Witkowski 2011b).

Baobabs are deciduous, bearing leaves and flowers in the wet season. Flowering lasts 4-6 weeks with a few flowers opening every night (Baum 1995). The fruit takes up to six months to mature and is usually ready for harvest at the peak of the dry season (Sidibe and Williams 2002). Fruit production averages 77±14 (SE) fruit per tree with wide variation between years, land-use types and individual trees (Venter and Witkowski 2011a). The fruit is a hard indehiscent capsule, containing a dry powdery pulp and 24-194, highly viable

(>89%) seeds, which form persistent seed banks (Venter and Witkowski, unpublished data). However, many populations show a positively skewed size-class distribution with poor natural regeneration, which appears to be severely hampered by poor rainfall and domestic livestock browsing (Venter and Witkowski 2010, unpublished data). In South Africa baobabs are listed as a protected species by the National Forest Act (DWAF 1998) and by provincial regulation (LEDET 2004).

2.3 Data collection and analysis

A series of interviews with 60 randomly selected baobab fruit harvesters were conducted from June to September 2009 in nine villages across the collection area (Fig 1). Two questionnaires were used, both covering five topics, the first in more detail and longer than the second. Thirty interviews were conducted using each type of questionnaire (30 + 30 = 60). Both questionnaires were vetted and approved by the University of the Witwatersrand Human Research Ethics Committee (H0 90302). The topics covered were: 1) respondent information and income, 2) household information, 3) NTFP use and income, 4) baobab product use, and 5) baobab ecology and management. In addition to general respondent information, the first questionnaire included detailed questions on the use of and income derived from NTFPs in general and baobab products in particular. The second questionnaire covered respondent information and broader perceptions of baobab use and management. Income values were recorded in South African Rands and converted to United States Dollars (US$) at the prevailing exchange rate of US$1=ZAR7.19, July, 2011.

Analysis and interpretation was done by categorizing the data by village type (large versus small); respondent age (16-29, 30-49 and 50+ years), income stream (social grant, informal, NTFP income-value, NTFP use-value), NTFP type and baobab product type. ‘Large’ villages had facilities such as shops, petroleum stations, clinics and schools. ‘Small’ villages were more remote and lacked these facilities. ‘Social grants’ refer to pension and child grants. ‘Informal’ income refers to income from part-time, non-skilled work and the vending of various goods as opposed to ‘formal’ income from full-time employment. ‘NTFP income’ refers to respondents who earn an income from collecting and selling NTFPs. In this context distinctions were made between income from baobab products in general (bark, fruit) and income from the sale of baobab seed for commercial purposes.

Following Dovie *et al.* (2002), the monetary value (direct-use value) of NTFPs was calculated. Locally quoted prices for each product were based on quantities such as a 250 ml cup, a litre bottle, head-load or pickup vehicle load, whichever was appropriate. This value was multiplied by the general frequency of use (or collection) of that portion over the course of the year and by the number of respondents using the product. Depreciation was

not included in the calculation because it only applied to two products (poles and thatch), the majority were food products which were used quickly. The following formula was used:

Annual use-value = sale value/portion x frequency of use/year x number of users.

T-tests, Mann-Whitney U-tests, Wilcoxon Matched Pairs test and Fishers Exact tests were used to compare differences between village types, between NTFP income and baobab seed income and between grouped income streams. ANOVA followed by Fishers Least Significant Difference (LSD), Kruskal-Wallis tests and Pearson Chi-Square tests were used to compare differences between age groups and income streams. Regression analysis determined if there was a relationship between baobab seed income and other NTFP income. Only one respondent was male, therefore analysis by gender was not done.

3. Results

3.1 Demographics of baobab fruit harvesters

Harvesters tended to be unemployed women, mostly aged between 30-49, with little or no schooling and with household sizes that varied between 1 and 12 people (Fig. 2). Many respondents were involved in the informal sector, working as labourers (20%) and vendors (35%) (Fig. 2). Social grants were received by 68% of respondents either in the form of pensions (18%) or child grants (50%) (Fig. 2).

3.2 Income from social grants and employment

There was no significant difference in annual income between social grants and informal income ($t=1.69$, $df=34$, $p=0.1004$), each making a 35% and 18% contribution to total income respectively (Fig. 3). The average social grant income in small villages was significantly higher than in large villages (Table 1), due to proportionally more elderly people receiving higher pensions as opposed to child grants in small villages (55% and 25% respectively). In contrast, respondents in large villages tended to earn more from informal income than respondents in small villages, probably because of increased opportunities. Respondents >50 years of age received a significantly higher income from social grants than the ‘middle-aged’ (30-49 year) and ‘young’ (16-29 years) (Table 2). This is expected, as pensions are larger than child grants. Middle-aged respondents tended to earn more from informal income than young and elderly respondents (Table 2).

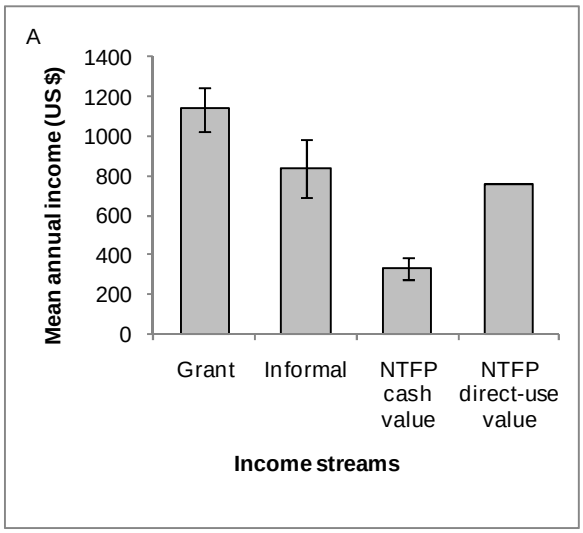

Figure 3. Annual income (mean ± SE) and direct-use value received by harvesters that have social grants, informal income (traders and vendors), who sell Non-Timber Forest Products (NTFPs) and who use NTFP.

Table 1. Comparison of income streams between small and large villages. Fisher's Exact test indicates differences between the numbers of people involved in each income stream between villages. Mann-Whitney U-test indicates differences in the amount earned from each income stream between villages.

Village sizes	Annual Income (US$) Small Villages		Annual Income (US$) Large Villages		Fishers Exact test	Mann-Whitney U-test	
Income Stream	mean±SE	n	mean±SE	n	p	Z	p
Grant Income	1292±123	17	829±95	24	0.4803	2.7891	0.0062*
Informal Income	596±95	7	916±133	21	0.0246*	0.8895	0.3737
NTFP Income	312±133	9	252±64	15	0.2035	-1.0257	0.3051
Baobab Income	167±26	13	108±10	17	-	1.668	0.0953
Total income	1656±211	13	1521±228	17	-	0.4813	0.6301

Table 2. Comparison of income streams between age groups. Pearsons X2 indicates differences between the number of people involved in each income stream between age groups. Kruskall-Wallis test indicates differences in the amount earned from each income stream between age groups.

Age groups	Annual Income (US$) Age 16-29 years		Annual Income (US$) Age 30-59 years		Annual Income (US$) Age 50+ years		Pearsons X^2		Kruskal-Wallis	
Income Stream	mean±SE	n	mean±SE	n	mean±SE	n	X^2	p	H	p
Grant Income	787±96	7	787±81	21	1525±142	13	1.5691	0.4563	14.8648	0.0006*
Informal Income	431±97	6	1024±151	17	684±93	5	3.6318	0.1627	6.4791	0.0392*
NTFP Income	443±201	6	233±59	14	267±49	4	6.3095	0.0427*	1.2906	0.5245
Baobab Income	81±12	7	154±22	15	139±23	8	-	-	5.3037	0.0705
Total income	1361±245	7	1482±257	15	1954±241	8	-	-	3.1842	0.2035

3.3 Income-value of NTFPs

The average annual income from the sale of NTFPs (including baobab seed) was significantly lower than from social grants (t=7.2742, df=49, p<0.001) and informal work (t=4.0381, df=43, p=0.0002) (Fig. 3). The overall cash contribution made by NTFP sales was 14% of total annual income, far less than social grants but close to the contribution from informal income. There was no significant difference in income from NTFPs between income groups (H=2.56, *p*=0.4643) (Fig. 4). The highest proportion (43%) of NTFPs sales were to outside traders. Otherwise 33% sold NTFPs to people from the same village and 20% to neighbouring villages. A significantly lower proportion (7%) of respondents were traders themselves (i.e. travelling to towns or cities outside the area to sell products) versus those who sold locally or to traders who came from outside (χ^2=13.38, df=3, *p*=0.0039). A similar proportion of respondents were involved in selling NTFPs in small and large villages and the income earned from the sale of these products tended to be higher in small than large villages (Table 1). A significantly higher proportion of respondents aged 30-49 years were involved in selling NTFPs (excluding baobab seed) than younger and older respondents (Table 2), yet younger respondents tended to earn more than older age groups (Table 2).

Due to the differences in cash value and proportion of people involved in the sale of NTFPs, the proportional contribution made to total income differed between products (Fig. 5).

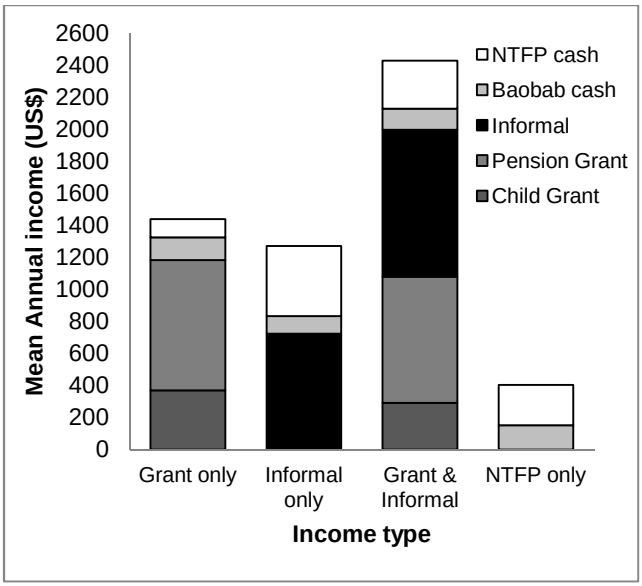

Figure 4. Income (grant income, informal income, NTFP cash income (excluding baobab seed) and cash income from baobab seed) by income type (those receiving annual grants only, involved in informal employment only, those receiving both grants and informal income and those that have neither grants nor informal income and thus depend on NTFP for their cash income.

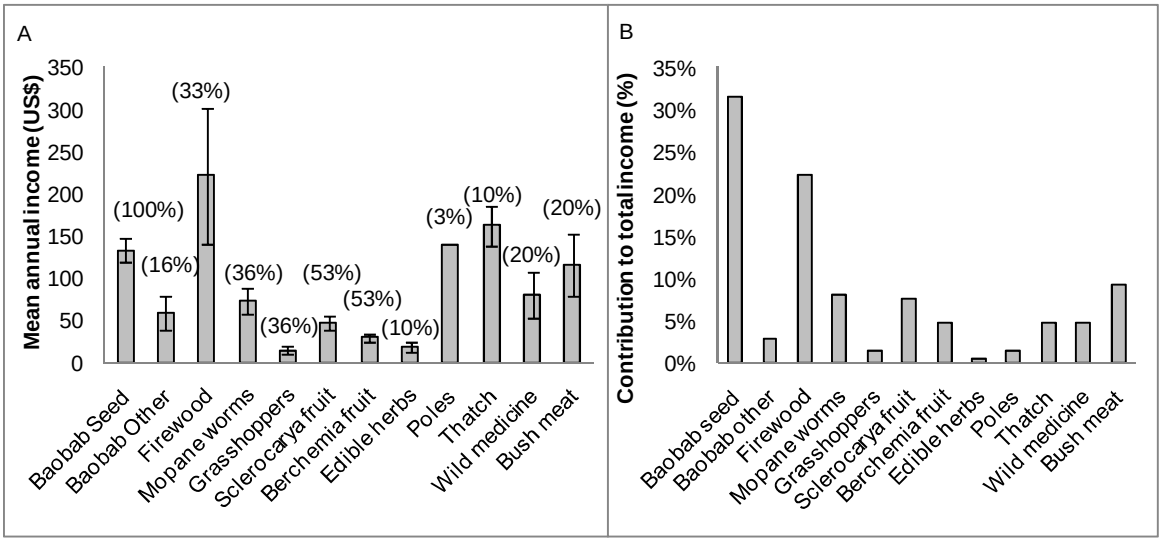

Figure 5. Annual cash income (mean ± SE) from NTFPs and percentage (%) of respondents who sell these products in brackets above each bar (A). The proportion of total cash income received from the sales of NTFPs across all respondents (n=30) (B).

3.4 Income-value of baobab products

Income from 'other' baobab products (mats, ropes, snuff holders and whole fruit), were sold by 16% of respondents and earned significantly less than from 'baobab seed' sales (t=-2.09, df=33, *p*=0.0447) (Fig 5). The mean annual income from baobab seed (US$136±14) was not significantly different to the combined mean annual income from other NTFPs (US$220±54) (T=190.50, Z=0.5838, *p*=0.5593 (Wilcoxon matched pairs test)) (Fig. 5), and made up 38% of total NTFP cash income (Fig. 6). No significant relationship was found between baobab seed and NTFP income (*p*=0.3260, R^2=0.0340), indicating that concentrating on baobab seed did not result in a lower (or higher) income than from other NTFPs. Respondents in small villages tended to earn more from the sale of baobab seed than respondents in large villages (Table 1) and middle aged and elderly respondents tended to earn more from the sale of baobab seed than young respondents (Table 2). There was no significant difference in income from baobab seed between respondents of different income types (Fig. 4) ($F_{(3,26)}$=0.28, *p*=0.8385).

Cash earned from the sale of baobab seed was used to buy a variety of goods in particular food (Fig. 7). Cash was spent by respondents in their village (45%), neighbouring villages (40%) and the large towns Thohoyandou and Musina (Fig.1)) (25%).

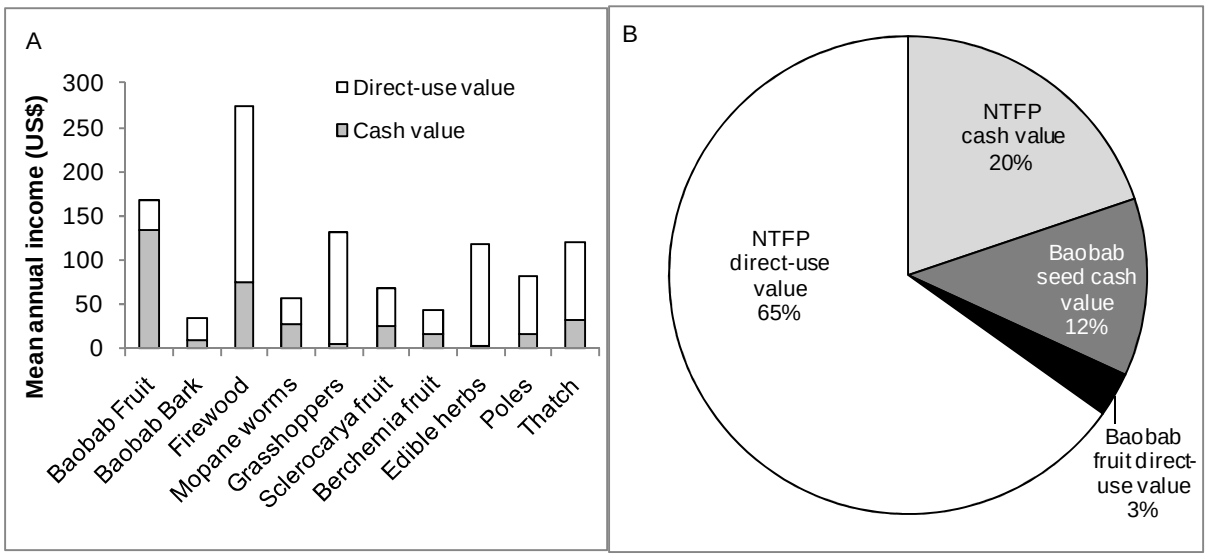

Figure 6. Cash value and direct-use value of non-timber forest products (NTFPs) (A). The proportional cash value and direct-use value of NTFPs and baobab seed and fruit (B).

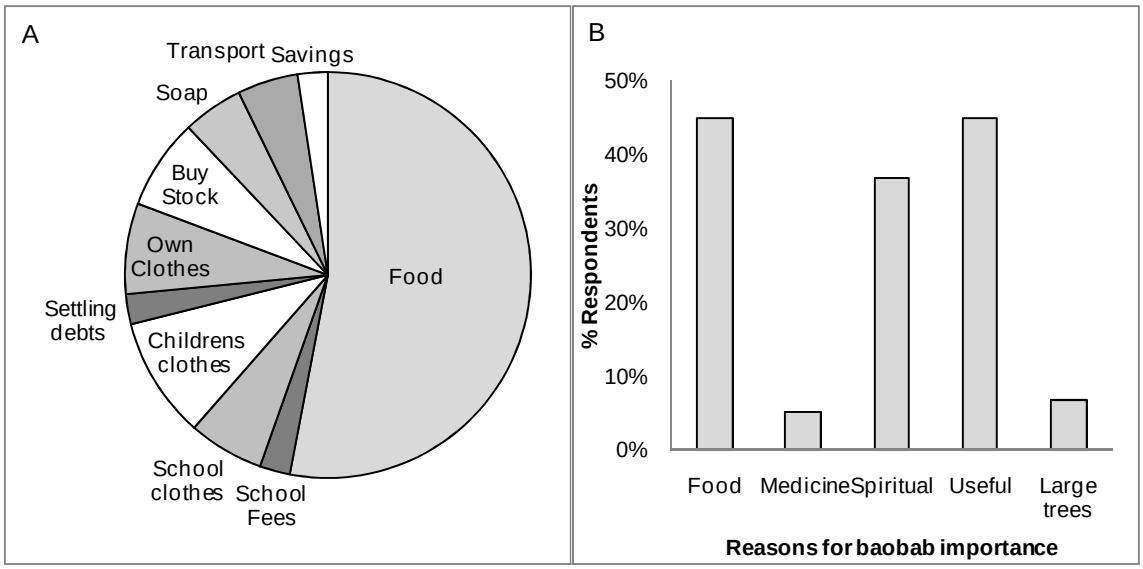

Figure 7. Uses of cash from the baobab seed sales (A) and the importance of baobab trees (B) reflected in the proportions of respondents.

3.5 Direct-use value of NTFPs

Annual direct-use value of all NTFPs was substantially higher than from the sale of these products (Fig. 6), contributing 33% to total annual income. Except for baobab fruit, all NTFPs had higher direct-use values than income values (Fig 6). The 'importance' of these products was determined by a combination of their frequency of use (subsistence value) and cash value (Fig. 8). A few respondents considered some NTFPs as 'not important', particularly those who did not sell or use the products. For example 10% of respondents

rated both mopane worms (phase of the mopane emperor moth *Imbrasia belina (*Kozanayi and Frost 2002)) and marula (*Sclerocarya birrea* subspecies *caffra;* (Helm et al. 2011)) as 'not important' because it was forbidden by the church to eat worms or drink alcohol made from marula fruit. Poles and thatch were rated as 'not important' because traditional houses were being replaced with 'modern' houses made of corrugated iron roofs. Furthermore 70% of respondents said that wild medicine was 'not important' because they went to government clinics (Fig. 8). These are interesting responses that possibly reflect a change in culture and economy.

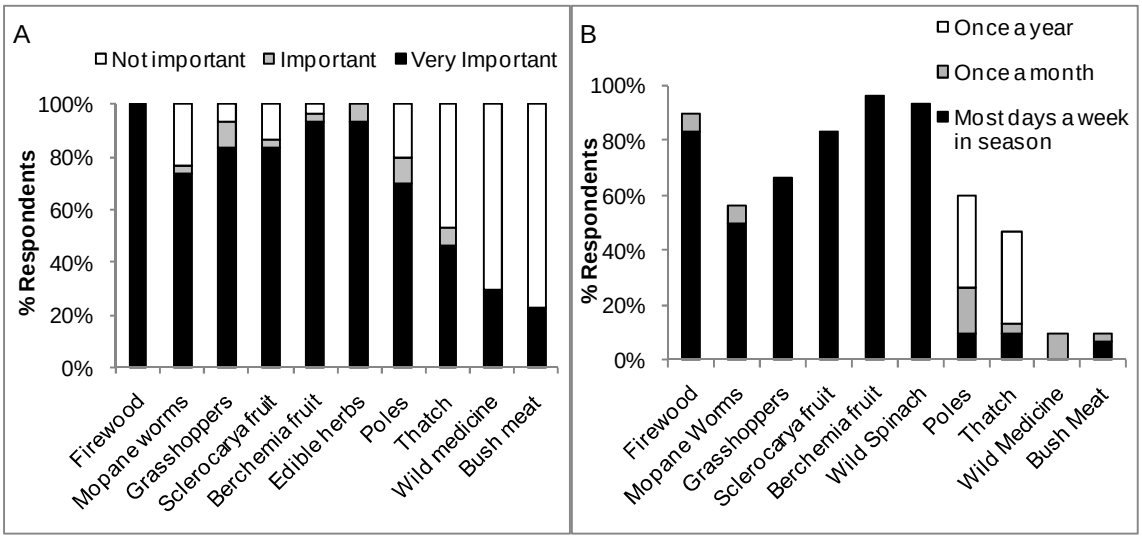

Figure 8. Percentage (%) of respondents who indicated the relative importance (A) and frequency of use (B) of Non-Timber Forest Products (NTFPs).

3.6 Use-value of baobab products

Baobab fruit was the only NTFP that had a cash value 4x higher than its direct-use value (Fig. 6). The direct-use value formed 4% of the total direct-use value of other NTFPs. All respondents said that baobab fruit was important both in the past and in the present (Fig. 9). Income generated, from the sale of seed, was important as a source of cash for all respondents and 22% added that it helped alleviate poverty in the community. Its use as a food item was reported by 73% of respondents. Fruit pulp could be mixed with milk to make 'yoghurt', with water to make ice lollies or added to porridge to give it a sour taste. The outer husk of the fruit was carved by 17% of respondents to make a snuff holder. It was used by 7% of respondents as kindling and 13% burned the husk to make 'soda' which is added to spinach giving it a slimy texture.

The majority of respondents collected fruit from plains, rocky outcrops and fields in the communal rangelands, and significantly fewer obtained them from trees within the village

(χ^2=47.95, df=3, p<0.001) (Fig. 9). Those that did collect fruit in villages tended to collect them from their own home trees rather than from general village trees (Fig. 9). All said that fruit was collected from under trees, and 3% also threw sticks to dislodge fruit from trees. Most (90%) respondents walked to collect fruit and far fewer (10%) also used donkey carts, hired at R60 per day, to help transport the fruit back to villages.

All respondents said that baobab bark was an important product in the past, but 57% felt that bark was no longer important because it had been replaced by nylon rope (Fig. 9). Seventeen percent of respondents used baobab bark rope for roof construction, 20% for bundling firewood, tying domestic animals, making whips, weaving baskets and mats and the ends of palm-frond brooms. Three percent said that babies were bathed with a bark infusion to give them strength. All respondents who collected bark said that it was harvested from juvenile trees which have stronger fibres than adult trees. The cash value of baobab bark was lower than its direct-use value and most other NTFPs (Fig. 6).

Baobab leaves were not considered important (Fig. 9) as only 6% of respondents ate young leaves and 40% used the leaves as fodder for livestock in times of drought. No respondents collected baobab leaves to sell.

Concerning baobab seedlings, 23% of respondents said that they could be eaten (Fig. 9), but that they were not an important product. Thirteen percent said children eat seedlings and two respondents (out of thirty) said they ate seedlings when they were thirsty, but very rarely.

No other baobab products were mentioned in the interviews.

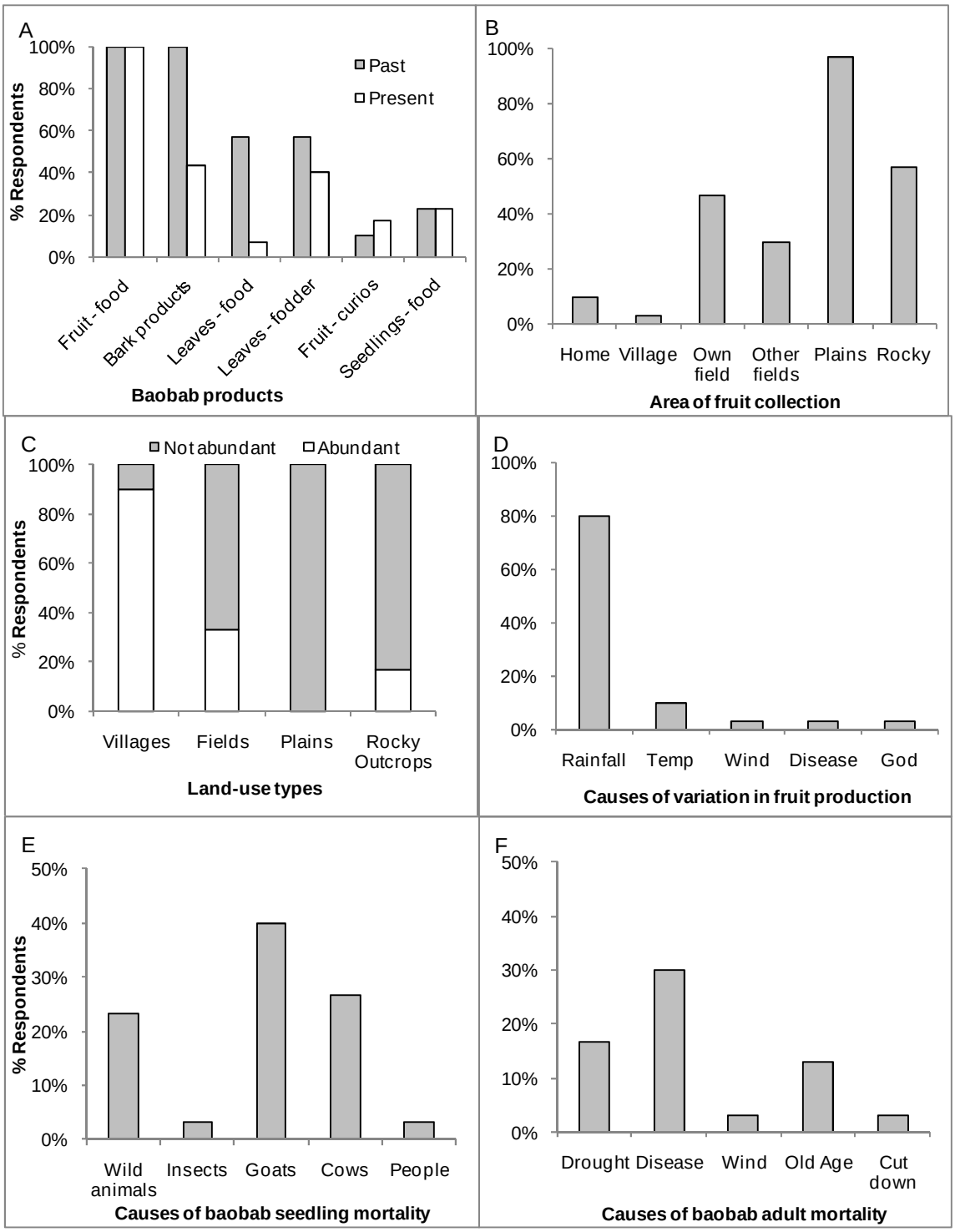

Figure 9. The percentage (%) of respondents who indicated importance of baobab products (A), who collected fruit in different areas (B), who indicated abundance of trees (C) causes of variation in fruit production (D), of sapling mortality (E) and of adult mortality (F).

3.7 Perceptions of baobab ecology, use and management

Apart from the cash earned from baobab seed sales, respondents said that baobabs were important for a variety of reasons (Fig. 7). All respondents said that cutting baobab trees down was not allowed by both government and traditional leaders.

Most respondents said that harvesting bark (73%), leaves (77%) and fruit (100%) did not damage trees, while 13% said that removal of fruit would affect recruitment. Respondents said that there were 'lots' of baobabs in the plains, rocky outcrops and fields, and 'few' in villages (Fig. 9). Baobabs were believed to live for over 1000 years by 46% of the respondents, and 27% said that they lived forever. All respondents said that fruit production varies from year to year, and most felt this was because of rainfall (Fig. 9). That not all baobabs produce fruit was believed by 92% of respondents. Most, 92% recognised this was because there were male and female trees while 8% could not give a reason.

All respondents said they regularly saw baobab seedlings and 37% that the seedlings would disappear after the rains. Domestic animals, followed by wild animals and lack of rainfall were believed to be the main threat to seedling survival (Fig. 9). Baboon predation of immature fruit was seen by 3% as a problem for recruitment. As many as 70% of the respondents had seen one dead baobab over the last ten years, most of which had died of disease or drought (Fig. 9).

Respondents said that baobabs in homesteads and fields were owned by the individuals on whose land they grew, and trees outside these areas were not owned by anybody. Only 3% had planted a baobab, all of them at their homes. All respondents felt it was not necessary to plant baobab trees, but that if they were given a tree they would plant it either at their home (67%) or in their field (37%).

4. Discussion

This study has shown that the cash value derived from the sale of baobab fruit for commercial utilization is four times higher than its direct-use value. The annual cash income received from baobab fruit alone made up 38% of the total annual sales of all other NTFPs. Similarly, in other parts of southern Africa the sale of baobab fruit for commercial purposes has been reported to increase the monthly cash income of individuals by 250% during the harvesting season (Gruenwald and Galizia 2005). Previous to commercialisation, the cash value from the fruit was negligible. As a subsistence product, the use of baobab fruit has diminished and now has a lower direct-use value than other NTFP food items.

All respondents said that income from the sale of baobab fruit was very important and helped alleviate poverty. In arid environments, such as where the research was done, the relative importance of this income may be higher than in moister areas, where there

would be a greater variety of NTFPs available and where subsistence agriculture is more reliable. Cash is becoming more important in maintaining standards of living and access to cash helps move households out of poverty by giving them opportunities to participate in a more lucrative economy (Cavendish 2000). As was seen in this study, downward trends in the use of some NTFPs such as poles, thatch and medicine indicate that there is a greater reliance on cash payments for many livelihood needs such as increasing costs of food, education and transport. Furthermore, it was seen that cash was used for investing in informal income sources by buying stock to expand businesses, and in savings, reflecting a trend found in communities moving from a subsistence into a cash economy (Belcher *et al.* 2005). Thus the contribution of commercial baobab harvesting plays an important role, not only in alleviating poverty, but also empowering marginalized people to keep up with a 'modern' world or as a stepping stone to a more secure livelihood.

The direct cash benefits from the commercialization of baobab fruit has been clearly shown in this study. However, the implications of commercialization need to be carefully considered. Firstly, does commercialization affect current, albeit low, subsistence use of baobab fruit? Secondly, how will commercialization affect access to the resource and the benefits currently enjoyed by the marginalized section of this community? Thirdly, how does commercialization affect sustainable harvesting; and lastly, can this value be improved for local harvesters?

In West Africa the value of baobab products for subsistence purposes, was rated by local people as much higher than its commercial value (Buchmann *et al.* 2010). However in Venda it was acknowledged that there was a much lower use of baobab products than in the past, independent of any commercial value. However, baobab fruit pulp is high in vitamin C and calcium, and its use contributes to a healthy diet (Chadare *et al.* 2009). Even though its use is very low, any large-scale sale of the fruit may result in scarcity and a lower intake of pulp and these negative impacts on health should be quantified.

It has been found elsewhere that income gained from the sale of NTFPs helps women increase their status in the community, as they make a contribution to household income and improve their personal circumstances. But if returns are recognized as high, these women could be edged out by men or by richer people in the community (Lybbert *et al.* 2002; Shackleton and Gumbo 2010). Access to baobabs is determined by ownership of the land on which they grow, but this only applies to a small proportion of the trees; access to trees outside such areas, constituting the highest number of trees, are accessible to all members of the village. Although outsiders do not have access to these resources without prior permission of the chief, these rules are not clearly protected and commercialization may turn commonly-shared resources into resources 'owned' by businessmen, powerful elites or outsiders.

As baobab fruit becomes more valuable, clear and broadly-accepted rules of access will need to be established so that the harvesters currently benefitting from the resource continue to do so in a fair and equitable way. Regulatory frameworks should define who has access to which kind of resource and should determine how benefits, collection and trade are shared among stakeholders (Shackleton and Gumbo 2010). In southern Africa, institutional structures that manage resources are weak, often leading to overharvesting and poor management of resources (Ticktin 2004). South Africa has instituted legislation that protects local people's benefits and rights to their resources (DEAT 2008) during commercial (or bio-prospecting) activities. However, on communal land 'ownership' of resources is open to wide interpretation, making the rights of current beneficiaries vulnerable despite this legislation (Crouch *et al.* 2008).

If the livelihoods of rural people, who rely on NTFPs, is to be maintained, sustainable utilization is essential. Thus take-off rates should not damage the productive potential of the resource (Peters 1996). The term 'ecological tolerance' is used to describe the degree to which plant populations can recover from harvesting (Ticktin 2004). Many studies have found that the utilization of NTFPs is unsustainable (Boot and Gullison 1994; Ticktin 2004; Venter 2004). However, fruit and seed harvesting generally exhibits higher degrees of tolerance (Zuidema and Boot 2002; Emanuel *et al.* 2005). This depends on three factors: firstly, the protection of parent trees; secondly, continuous recruitment; and thirdly, the longevity of the plant. Baobabs are long-lived trees and, once mature, can continue to produce fruit for many hundreds of years. Fruit harvesting neither damages nor kills trees, and thus annual harvests can be maintained. At the same time, recruitment is generally poor and sensitive to fluctuations in rainfall and browsing pressure (Venter and Witkowski unpublished data), so it can be argued that removal of seed may hamper recruitment. Fruit harvesting should thus be combined with a propagation and planting program to mitigate any adverse effects on recruitment.

Collection of other baobab products, notably bark and leaves, are more destructive and concerns have been raised about their sustainability (Romero *et al.* 2001; Schumann *et al.* 2010). Bark harvesting for subsistence use (low frequency) does not result in tree mortality, however, where bark harvesting is done for commercial purposes, frequencies are too high for trees to recover adequately, jeopardizing the survival of parent trees and affecting fruit production (Romero *et al.* 2001). Harvesting baobab leaves, and in so doing deliberately pruning trees to stimulate further leaf production, also hinders fruit production (Schumann *et al.* 2010). Without adequate institutional structures to manage and control harvesting, the commercialization of bark and leaf products should not be encouraged in Venda.

Trade channels for raw ingredients, fruit pulp and seed oil, are fairly short and simple, with processors buying directly from harvesters. A further way to increase benefits to rural people would be local beneficiation of the product whereby investment in local post-harvest processing and packaging is made. Currently this is not being done due to lack of knowledge and infrastructure available at the local level (Welford and Le Breton 2008; Chadare *et al.* 2009)

Domestication is another way to increase benefits, and it has been shown that grafting adult material onto seedlings can produce flowers within 10 years (Jensen *et al.* 2011). In many parts of southern Africa water resources are extremely scarce and, if successful grafting depends on irrigation, this may not be a practical solution in this semi-arid region. Nonetheless, as the value and demand for baobab fruit extracts increase, suitable sites could be found and southern Africa could follow the lead of West African initiatives in domestication and cultivation (Jensen *et al.* 2011). The downside is that large scale plantings in agricultural settings are likely to bring prices down, resulting in poorer returns for rural harvesters. Nonetheless, at this stage the harvesting of wild fruit is considered more cost effective than cultivation (Gruenwald and Galizia 2005) and has other benefits like *in situ* conservation of communal lands.

Harvester's perceptions of baobab ecology and the results of ecological surveys (Venter and Witkowski 2010, 2011a, unpublished data) were very close, indicating that both have a similar understanding of the resource base. Harvesters said that there were fewer trees in natural areas than in villages and fields and although population surveys show higher densities in the latter (Venter and Witkowski 2011b), the relatively small sizes of villages and fields would mean that there were indeed fewer trees in total. Respondents were aware that fruit production varied from year to year, and annual fruit production surveys found the same. Although ecologists could only speculate on the causes of this variation, harvesters said it was due to lack of rainfall. Ecological surveys also found that many trees consistently produced fewer fruit than others (Venter and Witkowski 2011a) and harvesters confirmed this, and referred to these trees as 'male' trees. Such a perception was also recorded among people in West Africa (Assogbadjo *et al.* 2008). Respondents said they often saw baobab seedlings, especially in times of good rainfall, but that they quickly disappeared due to domestic animal browsing. This, too, is consistent with patterns found by Venter and Witkowski (unpublished).

5. Conclusion

Commercialization of baobab fruit is valuable to rural people in southern Africa. Cash generated from the sale of baobab fruit helps alleviate poverty, improve livelihoods and

allows participation of marginalized people in a growing cash economy. Direct-use value of the fruit is low and thus commercialization is not expected to have significant impact on subsistence use. Rights of access to the resource are not clearly defined and as the resource grows in value, the lack thereof may jeopardize current benefits to marginalized people, thus workable regulatory frameworks need to be put in place to secure these rights. Furthermore, benefits can be increased by investing in post-harvest processing. Lastly, fruit harvesting is non-destructive, and thus has high ecological tolerance, however the negative effect of seed removal on recruitment, requires investment in propagation and planting programs.

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Chapter 8

To be submitted

Using a deterministic population model to evaluate the effects of fruit harvesting and livestock on baobab (*Adansonia digitata* L.) populations in five land-use types

Abstract

The subsistence and commercial use of baobab (*Adansonia digitata*) fruit is important to many thousands of marginalized people in the arid tropics of Africa, yet sustainable harvest levels have not previously been studied. Size-class distributions of baobab populations tend to be stable, suggesting high tolerance to harvesting. However, environmental conditions have changed substantially over the last 100 years. Increasing livestock numbers, land modification and climate change are new threats which may affect tolerance to fruit harvesting. To investigate this, a deterministic stage-based population projection matrix model was developed using (a) long term baobab monitoring data from 2 sites, (b) radiocarbon age calculations, (c) extensive field surveys of population structure and fruit (and seed) production, and (d) experimental field trials on seed banks and seedling and sapling survival in relation to the presence of livestock. Projected population growth (λ) was then evaluated for five land-use types (nature reserves, rocky outcrops, plains, fields, and villages) under three levels of livestock (none, moderate and high stocking rates). Response to fruit harvest intensity was tested for each scenario by decreasing seed availability by 10% from 100%. High livestock numbers resulted in baobab population declines, with $\lambda<1$ in all land-use types. Under moderate and zero livestock numbers, baobab populations in plains, rocky outcrops, villages and fields were able to tolerate between 33-90% fruit harvest rates. In nature reserves there was already high predation on immature fruit by baboons and other animals, another cause of population decline, with the model showing no tolerance whatsoever to fruit harvesting. These results show that fruit harvesting can be sustainable in production landscapes under moderate livestock levels. However the future is uncertain, as a predicted lowering of rainfall due to climate change is a further concern, with likely negative impacts on fruit yields and consequently population projections. Thus active planting and protection of seedlings should take place to mitigate current and future negative impacts facing baobab populations.

Key words

Baboons; climate change; matrix model; planting; recruitment; rainfall; seedling protection; tolerance level.

1. Introduction

Sustainable utilization means, essentially, that take-off rates should not damage the productive potential of the resource, and that harvesting can be maintained indefinitely (Carter, 1996). The term ‘ecological tolerance’ is used to describe the degree to which plant

populations can recover from harvesting (Ticktin, 2004). Many studies have found that the utilization of NTFP (non-timber forestry products) is unsustainable at current levels of harvest (Hall and Bawa, 1993; Peters, 1996). However, the harvesting of fruit and seed has the least impact on population structure with high degrees of tolerance, except for non-sprouting species. For long-lived tree species, extraction rates of between 86-92% are commonly calculated (Bernal, 1998; Zuidema and Boot, 2002; Emanuel *et al.*, 2005). High tolerance levels are attributed to four factors: fruit harvesting does not damage the plant itself; adult trees have high survival potential; recruitment is continuous, even if episodic; and trees are long-lived with extensive reproductive periods.

Baobab fruit are being wild-harvested for commercial and subsistence use in many parts of Africa, and this has become very important to the livelihoods of thousands of marginalized people (Buchmann *et al.*, 2010)(Chapter 7). Recently the global demand for baobab fruit derivatives, namely fruit pulp and seed oil, has grown substantially with exports to Europe, Asia and North America. This has made significant contributions to alleviating poverty and yet sustainable harvest levels have not been evaluated (Gruenwald and Galizia, 2005)(Chapter 7). Due to the long history of human use of baobab fruit, its importance as a subsistence product and the stability of baobab populations, the impact of fruit harvesting has seldom been of concern (Wickens, 1982; Venter and Witkowski, 2010). However, recent changes in the environment, such as land cover and land use changes (Coetzer *et al.*, 2010), increasing livestock numbers and climate change have raised the alarm about the future of baobab populations (Dhillion and Gustad, 2004; Cuni Sanchez *et al.*, 2011) (Chapter 6).

In many parts of Africa poor baobab recruitment is associated with high livestock numbers (Dhillion and Gustad, 2004; Chirwa *et al.*, 2006). In Chapter 6 it was found that consumption and trampling by livestock resulted in up to 87% sapling mortality. Poor rainfall and drought are also known to severely reduce recruitment and can lead to adult tree death (Gijsbers *et al.*, 1994; Caplan, 1995; Maranz, 2009) (Chapter 6). A loss of up to 85% of fruit has been found in areas where baboons predate immature fruit and this, too, may contribute to poor recruitment in some land-use types (Venter and Witkowski, 2011a). Furthermore, climate change predictions suggest that current suitable habitat for baobab populations in Africa could be reduced by up to an alarming 95% (Cuni Sanchez *et al.*, 2011). In light of these threats, there is clearly a need to re-assess the state of baobab populations and to evaluate the impact that baobab fruit harvesting will have on these populations in the future.

Population projection matrix models can be used to understand plant population dynamics, the importance of different life history processes and to answer ‘what if’ questions within different scenarios (Desmet *et al.*, 1996; Drechsler *et al.*, 1999; Caswell, 2001). They can be used to assess the impact of different levels of harvesting and determine the

maximum harvest intensity that a population can tolerate (Bernal, 1998; Emanuel *et al.*, 2005). The advantage of such models is that they have a standardized form, relatively low data requirements and can quantitatively predict the direction of population change in response to changes in fecundity, growth and survival (Desmet *et al.*, 1996; Caswell, 2001).

A study aimed at assessing the sustainability of baobab fruit harvesting was initiated in 2006. This study evaluated population size, fruit production, phenology, recruitment and socio-economic impacts (Venter and Witkowski, 2010, 2011a, b)(Chapter 5, 6 and 7). This paper draws on the ecological knowledge gained from these and other long-term studies, by using a deterministic stage-based population projection matrix model in five land-use types to determine population trends under different levels of livestock numbers and fruit harvest levels. Due to the long-lived nature of baobab trees, their high seed production and low adult mortality, it was predicted that there would be tolerance to very high (>90%) fruit harvest levels, but on the other hand the impact of poor recruitment would substantially reduce population tolerance, and require active mitigation and management.

2. Materials and methods

2.1 Study area

Northern Venda is situated in the north eastern section of Mutale District Municipality, Limpopo Province, South Africa (Fig 1). It forms part of the former Venda homeland where ownership and management of natural resources is the responsibility of traditional structures, civic organizations and government. The local population is mostly of the BaVenda ethnic group (Stayt, 1931), numbering just over 100 000 people with low levels of employment and education (Statistics-S.A., 2001).

The area is made up of five land-use types, namely; nature reserves, rocky outcrops, plains, fields, and villages. Nature reserves are under the control of provincial authorities and where the conservation of plants and animals is the main management objective. Plains and rocky outcrops are used as communal grazing lands; fields are used for dry-land cropping, and villages are densely populated, consisting of closely-spaced houses with electricity and communal taps. Livestock densities are generally high in villages were they are kept night.

Venda has a semi-arid summer rainfall regime with a mean annual precipitation of between 334-423mm (Mucina and Rutherford, 2006). Summers (i.e. October-March) are hot, winters (April-September) are mild, and frost seldom occurs. The soils are mainly derived from standstone, basalt and aeolian deposits (Brandl, 1981) in a gently undulating topography averaging about 400m above sea level. This study area falls in the Mopane and Lowveld Ecoregions of the Savanna Biome (Mucina and Rutherford, 2006). Wildfires

seldom occur, due to a prevalent low fuel load. Wildlife is scarce outside of the nature reserves, and elephants are now infrequent visitors.

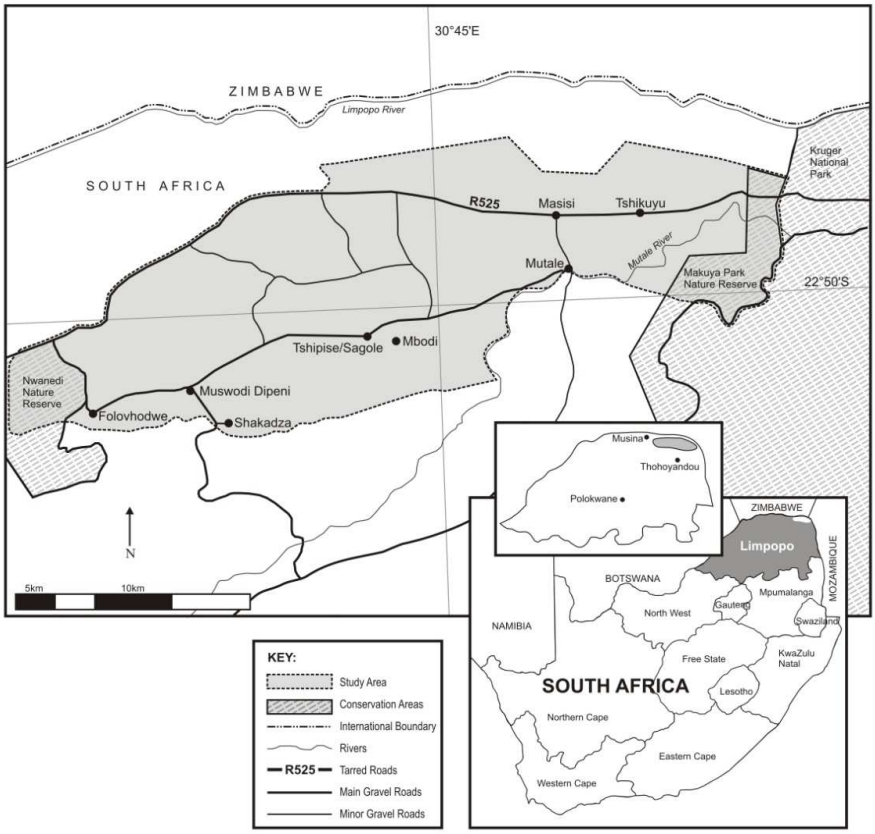

Figure 1. Map indicating location of study area in Limpopo Province, South Africa

2.2 Study species

Baobabs (*Adansonia digitata* L., family Malvaceae, subfamily Bombacoideae) are distributed widely across Africa south of the Sahara, where they are associated with the drier plant communities of the Sudanian and Zambezian lowlands (Wickens and Lowe, 2008). The northern part of South Africa forms the southern limit of their distribution. Here baobabs are closely associated with vegetation dominated by *Commiphora*, *Grewia* and *Colophospermum mopane* (Venter and Witkowski, 2011b) and have the highest densities in villages, followed by fields, plains and rocky outcrops. Baobabs are known to be extremely long lived, reaching up to 1300 years of age (Patrut *et al.*, 2007). Analysis of size-class distributions suggests that baobab populations in all land-use types are stable with the result of episodic recruitment events (Venter and Witkowski, 2010).

Fruits start to form in December and they drop six months later, in May/June, which is when they are ready for harvest (Chapter 5). Fruit production varies significantly between

years and land-use types (Venter and Witkowski, 2011a) and is strongly determined by variations in flower numbers (Chapter, 5). This fruit is a hard indehiscent capsule consisting, in the study area, of 24-194 seeds embedded in a dry powdery pulp (Chapter 6). A high proportion (>89%) of seed is viable and forms persistent seed banks (Chapter 6), yet natural regeneration is poor, severely hampered by infrequent rainfall and livestock browsing (Chapter 6).

2.3 Methods and analysis

Following Caswell (2001), Desmet *et al.*(1996) and Emanuel *et al.* (2005), a deterministic stage-based population projection matrix model, was constructed. This is a Lefkovitch model based on life-history stages. Four baobab life stages were used: (1) seedling, (2) sapling, (3) juvenile and (4) adult. The following parameters were required to construct the model: *Pi*, the probability that an individual in life stage *i* will survive and remain in that life stage; *Gi*, the probability that an individual in life stage *i* will survive and grow into the next life stage and *Fi*, the probability of an individual's fecundity in life stage *i*. G_i, and P_i are determined by average duration (d_i) and survival probability (s_i) of an individual in life stage *i*. These transitions are represented graphically in a life stage graph (Fig. 2)

The duration of each life stage was determined as follows. Seedlings were regarded as newly germinated plants <1 year old, and saplings as plants 1-3 years old (Table 1). Venter and Witkowski (2011a) found that trees <100cm diameter breast height (dbh) (termed sub-adults) could be considered juvenile because fruit production was insignificant compared to that of trees ≥100cm dbh, which were then regarded as adults. To calculate the duration of juvenile and adult life stages, the growth rates of each stage was determined from two data sets: 1) accelerated mass spectrometry (AMS) radiocarbon dating results of local trees; ((Patrut *et al.*, 2010), Venter *et al.*, unpublished data) and 2) 80-year increment measurements (unpublished data) collected at Skelmwater Nature Reserve, near Musina, South Africa. First, the radiocarbon dated ages of three trees, one juvenile and two adults, and their corresponding tree sizes where used to calculate growth rates. Then growth rates of a further six juvenile and four adult trees were determined from the 80-year increment measurements. The average growth rate was thus calculated as 0.4 and 0.26 cm dbh/year for juvenile and adult trees respectively. The duration of each life stage (di) was determined by multiplying these growth rates by the following tree sizes: for juvenile trees 99cm dbh was chosen because this is the size at which juvenile trees become adults (Venter and Witkowski, 2011a); and for adult trees, 350cm dbh was chosen, because this the largest size-class that still represents a notable number of adults in the population (Venter and Witkowski, 2010). Results are given in Table 1.

Survival rates (s_i) for each life stage were determined from two sets of data. First, juvenile and adult survival rates came from 20-year monitoring data carried out in Musina Nature Reserve (unpublished data) and second, seedling and sapling survival rates came from Venter and Witkowski (Chapter 6). Sapling survival rates were calculated for plants that were protected from livestock and for plants that were exposed to high (but typical) livestock numbers. Thus it was decided to solve the matrix model for both these scenarios and to add a third level, half-way between, indicating moderate livestock numbers (Table 1).

F_i, fecundity, is a function of seed production, germination and seedling survival. Using data from Venter and Witkowski (2011a) and unpublished data (chapter 6 on recruitment), the following values were used for the different variables: percentage viable seed, 89% (the lowest %, so it is conservative); number of seed per fruit, 97 (medium-sized fruit); fruit-producing adults, 59%; seedling survival, 5% (from the plot study, Chapter 6) and seedling emergence percentage from sown seeds, 7%. Venter and Witkowski (2011a) determined the mean number of fruit per tree for each of the five land-use types in the study area (Table 1). Using these figures the matrix model was solved for each of the five land-use types.

Matrix parameters were determined using the following equations:

$$G_i = (s_i^{di}(1-s_i))/(1-s_i^{di})$$

$$P_i = ((1-s_i^{di-1})/(1-s_i^{di}))xs_i$$

F_i = (Seed/tree) x (% fruit producing trees) x (germination or emergence %) x (seedling mortality)

Using Microsoft Excel, these parameters were entered into the projection matrix (Fig.3), and the dominant eigenvalues (λ) calculated using poptools (Hood, 2010). This λ represents the relative stability of the population; if λ=1, the population is stable, if λ≥1 the population is increasing and if λ<1 then the population is declining (Caswell, 2001).

Eigenvalues (λ) were calculated for unharvested baobab populations in each land-use type and under the three levels of livestock browsing described above (5x3=15). To assess the impact of seed (through fruit) harvesting on the population, a sensitivity analysis was conducted by reducing seed availability in incremental reductions by 10% from 100%. The maximum allowable reduction of seed was reached when λ=1.

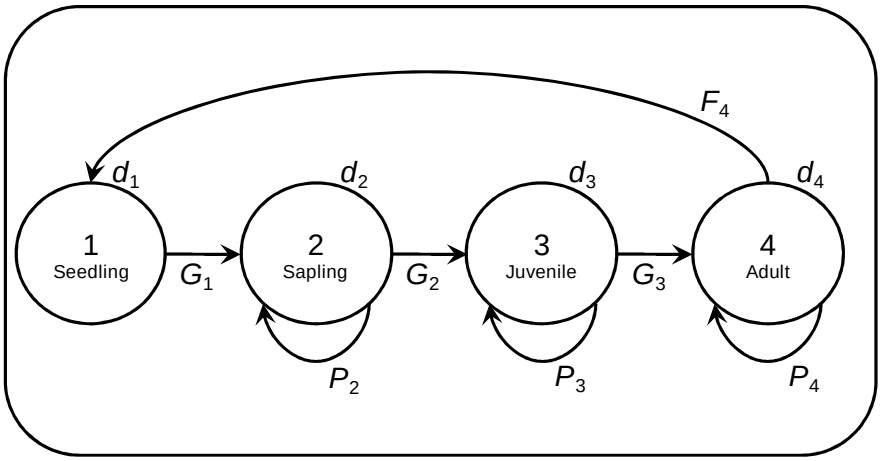

Figure 2. A four-stage life diagram for baobab. Nodes represent each life stage: seedling (N_1), sapling (N_2), juvenile (N_3) and adult (N_4). d_i is the number of years an individual spends in a life stage; F_i is fecundity; G_i is the probabity of an individual surviving through the life stage and moving on to the next stage; P_i is the probability of an individual surviving and staying in the stage.

$$\begin{pmatrix} P_1 & F_2 & F_3 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

Figure 3. A standard deterministic population projection matrix model based on a four-stage life diagram for baobab

Table 1. Time in life stage, survival and transition probabilities and fecundity for the four baobab life stages. Survival probabilities for the sapling life stage represent survival under three levels of livestock: no livestock, moderate livestock and high livestock. Livestock damage results from goat browsing and cattle trampling (Chapter 6).

Life stage	Time in stage (years) d_i	Survival probabilities si	Probability of moving to next stage Gi	Probability of staying in this stage Pi	Fruit production Fruit/tree	Fecundity Fi
Seedling	1	0.05*	0.05000	0.00000	0	0
Sapling (no livestock)	2	0.13*	0.40476	0.46524	0	0
Sapling (moderate livestock)	2	0.50	0.16670	0.33333	0	0
Sapling (high livestock)	2	0.87*	0.01496	0.11504	0	0
Juvenile	246‡	0.89**	0.00026	0.98118	0	0
Adult - Nature Reserve	1114‡	0.99**	0.00004	0.99630	2†	6.926547
Adult - Rocky Outcrops	1114‡	0.99**	0.00004	0.99630	13†	45.02255
Adult- Plains	1114‡	0.99**	0.00004	0.99630	29†	100.4349
Adult- Fields	1114‡	0.99**	0.00004	0.99630	88†	304.7681
Adult- Villages	1114‡	0.99**	0.00004	0.99630	90†	311.6946

* From Venter and Witkowski, unpublished

** From Musina 20 year data, unpublished

† From Venter and Witkowsi, 2011

‡ Derived from radiocarbon dating results and Skelmwater girth increment measurements (Patrut et al, 2011; unpublished)

3. Results

Parameters, P_i, G_i and F_i are given in Table 1. Figure 4 shows the decrease in λ under a range of simulated seed harvesting intensities for each land-use type and three levels of livestock number scenarios. Maximum harvest levels are indicated for each scenario where λ=1. Harvest level 0% indicates the pre-harvest population state for each scenario.

Figure 4 shows that the rate of population increase (λ) in nature reserves was <1 under all three livestock scenarios. In the absence of livestock and 0% harvest, λ=0.999, which is close to stable; thus any improvement in environmental conditions could improve the baobab population trend. The population in rocky outcrops is shown to be stable with no (λ= 1.008) or moderate (λ= 1.001) livestock numbers, and can tolerate 78% and 33% fruit harvest rates respectively (Fig. 4). Under high livestock numbers, the population shows a decline (λ= 0.999) with no tolerance to fruit harvesting. The population in the plains is stable, with no (λ= 1.016) and moderate livestock (λ= 1.006) numbers and can tolerate up to 90% and 70% fruit harvest rates respectively. Under high livestock numbers, the population is in decline (λ= 0.997) with no tolerance to harvesting (Fig. 4). Baobab populations in fields and villages, which produce the highest quantity of fruit (88 and 90 fruit/tree respectively) show similar results, with populations being stable with no (λ= 1.034) and moderate (λ= 1.016)

livestock numbers, and able to tolerate 96% and 90% fruit harvesting. Even with such high fecundity, however, field and village populations cannot increase under the current high livestock numbers (λ= 0.999) (Fig. 4), although they are close to stable.

High livestock numbers thus have a negative effect on population growth in all land-use types. If livestock numbers are kept at moderate levels, all baobab populations, except those in nature reserves, can tolerate fruit harvesting at levels between 33-90%. However the typical situation in communal lands is that livestock numbers are generally much higher than the commercial carrying capacity and it is unlikely that numbers will be reduced.

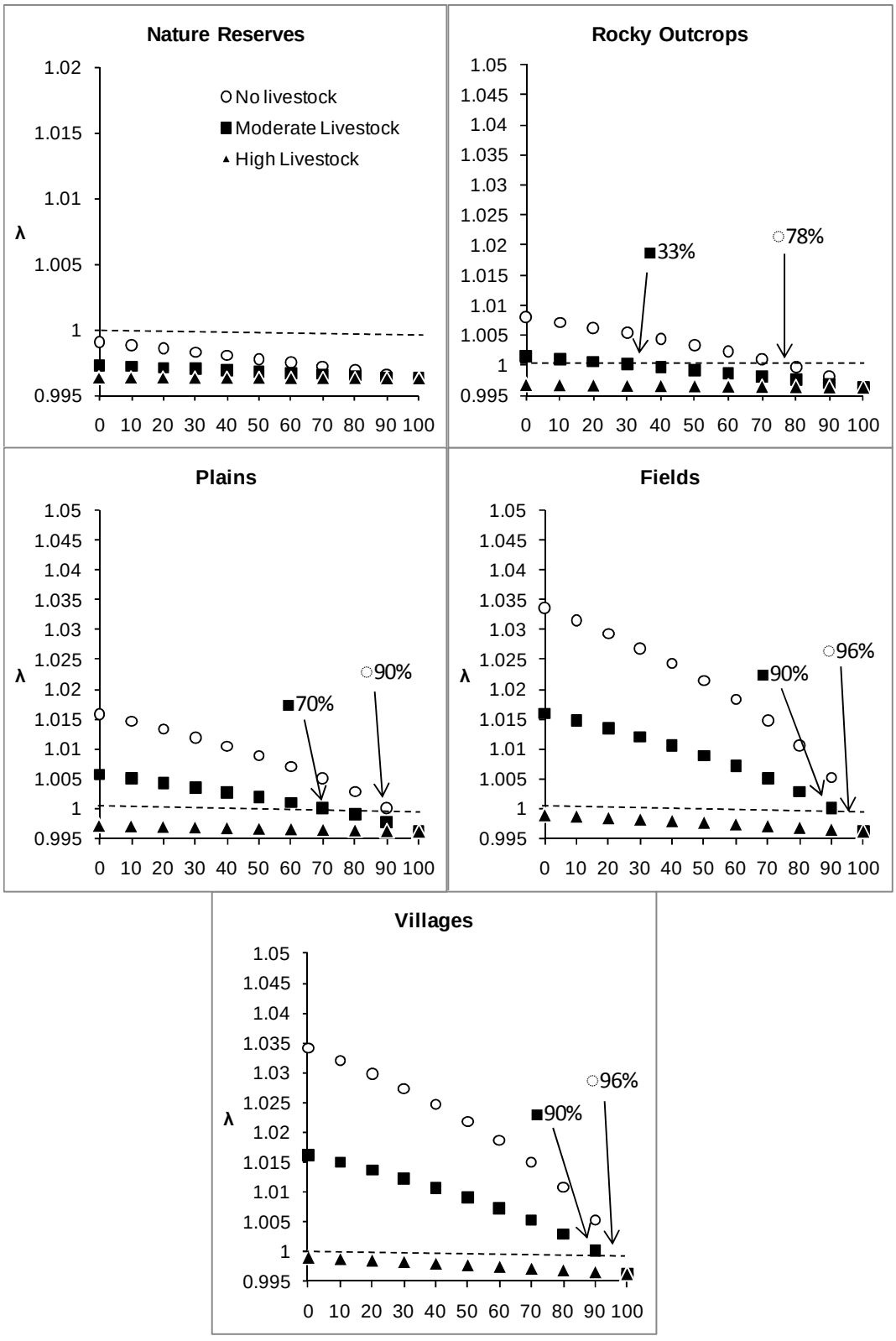

Figure 4. Change in projected population growth (λ) for each 10% increase in fruit harvesting at three levels of livestock (none, moderate and high) within five land-use types, nature reserves, rocky outcrops, plains, fields and villages. Maximum harvest levels (λ=1) indicated for moderate levels of livestock (filled square) and no livestock (open circles). At high livestock levels, all populations are in decline (λ<1). Nature Reserve population is in decline at all levels of livestock. Note different Y-axis scale for Nature Reserve. Percentage numerals in the figures represent estimates of allowable fruit harvest at population equilibrium.

4. Discussion

Dendro-demographic studies, using size-class distributions, show that baobab populations in the study area are stable (Venter and Witkowski, 2010) and that, because of the long-lived nature of baobab trees, episodic recruitment could maintain population levels. However, the output of the matrix model shows a different picture, with populations in most land-use types threatened by the current high livestock numbers. Size-class distributions reflect population trends in the past, whereas projection models use current circumstances to determine future rate of population increase or decrease (Desmet *et al.*, 1996). Furthermore, unlike stochastic models, deterministic models do not account for environmental variability and, in particular, episodic recruitment events that may take place in exceptional years. If an episodic recruitment event is able to make a substantial contribution to recruitment, then the population can be maintained under this life-history strategy, but in the face of climate change, land-transformation and growing human populations, successful recruitment events may not have a chance to occur again. The main factors found to drive predicted population declines are 1) baboon predation of immature fruit, 2) high livestock numbers and 3) low and potentially increasingly erratic rainfall.

The low fruit numbers in nature reserves are due to baboon predation of immature fruit early in the season when there is little other food available (Venter and Witkowski, 2011a). Our results show that this is a major contributor to population decline, as $\lambda<1$ even when there is no effect of herbivory or harvesting. However, there may be years when high or early rainfall provides alternative food sources for baboons (and other fruit predators), thus reducing pressure on immature baobab fruit (pers. obs.). This would allow baobab fruit to mature and potentially result in episodic recruitment that this model does not consider. Furthermore, baobabs have persistent seed banks and exhibit delayed germination (Chapter 6), this in addition to tree longevity means that populations are buffered by the 'storage effect', allowing them to persist through bad periods and increase in numbers again during better times (Lamont and Witkowski, 1995; Higgins *et al.*, 2000). Yet, it would still be prudent to have a conservative prediction concerning population growth when testing for sustainable harvesting, so as to provide for a margin of error.

High livestock numbers are shown to be a major cause of population decline. Results show that, even where fruit production is good, e.g. in villages and fields, populations would be unable to tolerate the current high livestock numbers. High numbers of goats and cattle are found around villages, where animals drink water and are kraaled (corralled) at night (pers. obs). On plains and rocky outcrops, livestock tend to spread out in search of forage with their browsing intensity becoming progressively less the further they

are away from villages (Grossman *et al.*, 1999). Fields exclude livestock except when fallow, but hoeing before the planting season also results in high sapling mortality (Dhillion and Gustad, 2004). This explains why, despite high baobab population densities and good fruit production, recruitment is poor in human-modified landscapes (villages and fields) in comparison to natural landscapes (plains and rocky outcrops) (Venter and Witkowski, 2011b).

Growth, germination and seedling survival are marginal in the study area, which is semi-arid with highly erratic seasonal rainfall (Schulze, 1997). Trees that are consistently watered (in gardens) grow exceptionally fast compared to those on the plains and are known to produce flowers within 23 years (Pardy, 1953), compared to the predicted average of 246 years in the study region. In nursery conditions, unscarified seed have germination percentages of between 20-50% in contrast to 0-7% found in the wild (De Villiers, 1951)(Chapter 6). Seedling mortality due to infrequent rainfall is 95%, but negligible in nursery conditions due to regular watering (pers. obs). Thus baobab populations found in areas of higher rainfall, such as parts of Malawi, Tanzania and northern Mozambique may be more stable than in more arid regions such as represented by the Limpopo Valley.

Adult tree mortality is another potential threat to baobab populations. Excessive bark harvesting for weaving can kill adult baobab trees (Romero *et al.*, 2001). In areas where elephants strip bark off baobabs, this too has lead to large-scale loss of adult trees (Barnes, 1980; Edkins *et al.*, 2007). Adult trees are also known to die when weakened by severe drought, excessive use of ground water, and disease (Piearce *et al.*, 1994; Caplan, 1995). Species with very long-lived adults have been shown to sustain populations for very long periods, as long as adults are not removed by land clearing (e.g. Drechsler et al. 1999) or are impacted upon by harvesting methods (or harvesting of critical tissues) or diseases that eventually result in mortality.

Baobabs are an important species, and their fruit will continue to be harvested for subsistence and commercial use. Fortunately, fruit harvesting *per se* has a relatively small impact on population stability and, in the absence of herbivory and other predation, baobabs will tolerate harvesting rates of up to 96%. Therefore mitigation of population decline should not only focus on reducing the impacts of fruit harvesting, but also on reducing the effect of predation, livestock numbers and climate change.

Mitigation can be attempted at three levels: direct harvesting interventions, additional management practices and landscape level management (Ticktin, 2004). Harvest-level mitigation entails control over the frequency and quantity of fruit collection. Fruit collection, staggered over time and between areas, allows trees to have rest years and release seed back into the environment. Limited allowable harvest per year would also allow a certain percentage of fruit to remain each year. However, it would be naive, in an open-access

situation, to expect harvesters to leave fruit on trees when there is cash to be earned. Furthermore, seedlings germinating from naturally dispersed seed may have a much lower chance of survival than hand-planted seeds and saplings (Witkowski and Lamont, 1997).

Sowing seed and planting saplings are additional management interventions that can boost recruitment. Saplings have a higher survival rate than seedlings (Chapter 6), but seed sowing does not need a nursery, which is expensive to run. Young plants would need to be protected until they escape the browse trap, e.g. by forming a 'cage with thorny branches' (using for example *Dichrostachys cinerea*) around them and thus should be planted in areas where they can easily be monitored, such as near fields and villages. At the same time, efforts should be made to include plantings in areas away from villages to reduce artificial clumping and to spread the risk of losing trees due to urban expansion and local catastrophes, such as fires or flooding. Care should be taken to use locally-sourced seed so as not to introduce unwanted genes. However, equally important is the use of seed from a wide variety of trees to avoid loss of genetic diversity. The use of truncheons and grafted trees also limits genetic diversity, and such trees have an artificial look, raising aesthetic concerns. Although grafted material has been shown to produce fruit much sooner than trees grown from seed (Sidibe and Williams, 2002), this requires additional water, a scarce commodity in these arid areas. In West Africa, local people have a culture of planting and protecting seedlings, presumably driven by the relatively quick return on leaf production, an important food source (Schumann *et al.*, 2010). In southern Africa, benefits are not immediate and population decline is treated as an externality; thus investing in nurseries and planting programmes may be necessary, even if costly.

At the landscape level, enhancing recruitment and controlling the activities that would affect fecundity and survival of adult trees, need to be considered. Lowering livestock numbers would have a direct positive effect on sapling survival, but livestock are important for many rural people and a reduction of numbers in order to enhance baobab recruitment is unlikely to be widely supported. The harvesting of other plant parts, such as leaves and bark, is known to reduce fruit production and increase tree mortality respectively (Romero *et al.*, 2001; Schumann *et al.*, 2010). The commercial harvesting of these plant parts should be strongly discouraged.

Finally, the impact of harvesting on ecosystems is a complex issue and not much is known about its secondary effects (Hall and Bawa, 1993). The removal of fruit may have an impact on fruit-eating animal species (Moegenburg and Levey, 2003). When mature fruit are available, baboons rely on these as a food source late in the season (Kunz and Linsenmair, 2007). In this area, elephants are infrequent visitors, but they do occur in other areas with baobabs; if harvesting took place there, this would reduce the fruit available to them. Frequent human visits to the trees during the harvest season may disrupt the wildlife that

roosts or nests in the baobabs, such as birds and small mammals (Wickens and Lowe, 2008). Studies aimed at better understanding these impacts will be important in guiding wider mitigation strategies.

The results of this paper clearly show that baobabs are sensitive to environmental change, and thus concerns over the future survival of the species should be taken seriously. It is predicted that climate change may substantially reduce suitable habitats for baobabs in the future (Cuni Sanchez *et al.*, 2011). There may be new areas where climatic conditions will become suitable, but due to land transformation and increased human population pressures, these areas may not be available for baobab establishment. Nature Reserves could remain the only refuges for baobabs, and assisted colonization into these areas may be necessary.

5. Conclusion

Baobabs can tolerate high levels of fruit harvesting of as much as 96%. However, predation on immature fruit by baboons in nature reserves and high livestock numbers associated with villages suggests that baobab populations in these land-use types are in decline. In the light of expanding human populations and climate change, management-level mitigation, through the active planting and protection of saplings is recommended to secure future baobab populations.

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Chapter 9

Synthesis and Conclusion

1. Introduction

The aim of this thesis was to study the biological and environmental factors that affect productivity (specifically fruit production) and recruitment trends of baobab populations in northern Venda, and to document the socio-economic benefits derived from the commercialization of the fruit. Knowledge and understanding gained from this study could be used to guide sustainable fruit harvest levels and to make recommendations for the management of the species. Figure 1 provides an illustration of the connections between the main components of the study and indicates which factors lead to population increase and decline.

This synthesis will do the following:

- Summarize the major findings of the thesis.
- Make management recommendations.
- Highlight the achievements and uniqueness of the study.
- Recommend future research areas.

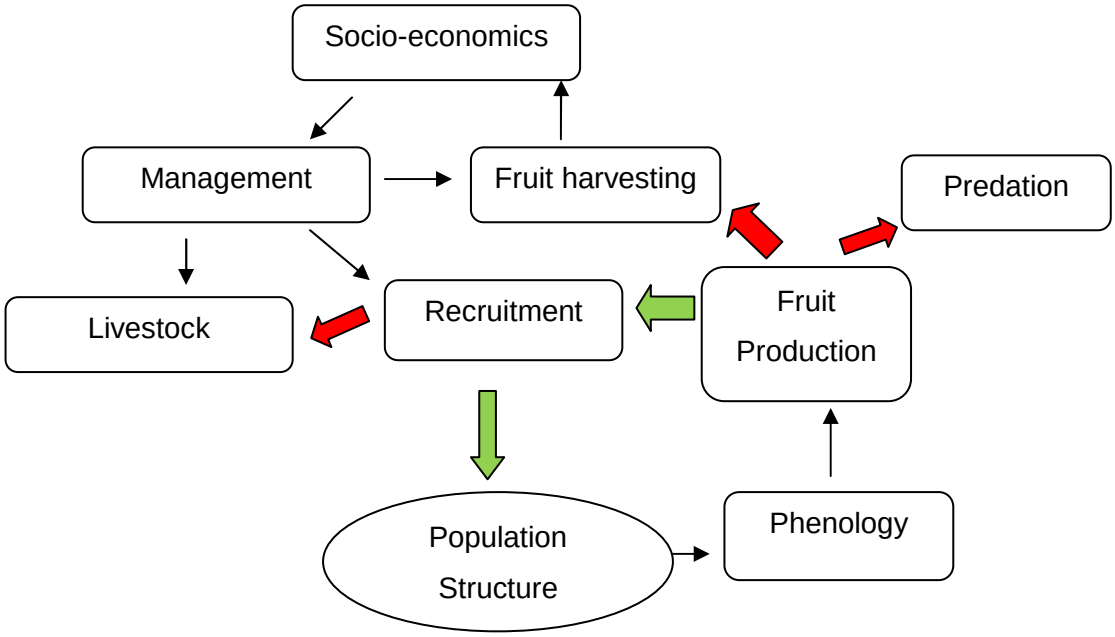

Figure 1. Flow diagram, illustrating the connections between the main components of the study. Red arrows and green arrows respectively represent factors leading to population decline and increase.

2. Summary of major findings

2.1 Population structure

The study revealed a number of important patterns and contrasts at land-use level (Chapters 2 and 3). The differences in the demographic patterns exhibited by natural and human-modified land-use types are particularly noteworthy. Data shows that adult trees in villages did not recruit as successfully as those on the plains. Villages had a significantly higher density of trees than did the plains, and yet had similar densities of juveniles. Paired t-tests confirmed significantly lower densities of juveniles to mature trees in villages but not in the plains. The SCD curve in the plains was more positively skewed than in the villages, which was confirmed by Kolmogorov-Smirnov tests and SCD slopes. Quotients showed a more stable population in the plains, and the permutation index was lower. The classic inverse J-shaped SCD is generally used by biologists as an indication of a healthy regenerating population; deviation from this would normally be a cause of concern. As a result, low recruitment rates and bell-shaped or positively skewed SCDs, which are typical of baobab populations across Africa, have led many authors to worry about the maintenance of baobab populations. However, due to the long-lived nature and extremely low adult mortality rate of baobabs, low recruitment rates may still be enough to maintain populations. It was concluded that the baobab population in northern Venda was stable and can be maintained by episodic recruitment events. However, the poor recruitment in human-modified landscapes called for further investigation.

Chapter 3 looked more specifically at populations in natural landscapes and at the difference in population structure between different vegetation types and soil types. There were significant differences in the densities of baobabs between broad-scale vegetation types with higher densities of trees in the Makuleke Sandy Bushveld than in the Musina Mopane Bushveld (Mucina and Rutherford, 2006). There were also significant differences between locally- identified, fine-scale vegetation types. Vegetation dominated by *Commiphora/Grewia* had the highest densities of baobabs compared to all other vegetation types, except for *Terminalia/Colophospermum* woodlands. When it came to soil types, densities were higher on sandy soils than on soils derived from basalt and aeolian deposits.

2.2 Fruit production

Yield per ha was substantially higher in human-modified landscapes (villages and fields) than natural landscapes. This is due the combination of significantly higher densities of trees (Chapter 2) and higher fruit production per tree (Chapter 4). Extremely low yields from Rocky Outcrops were directly attributed to baboon predation. Although yields from

plains was lower than villages and fields, the area represented by plains is vast and thus most of the fruit collected in a season comes from plains (Chapter 7).

The study (Chapter 4) highlighted number of other aspects related to fruit production. We found that stem diameter and crown size was poorly related to fruit production; thus these variables should not be used as predictors of fruit production. Fruit production differed between trees <100cm dbh and trees ≥100cm dbh, and it was suggested that a dbh of 100cm could be used to distinguish between sub-adult and adult trees in this environment. The study found that the greatest impact on mature fruit production was the result of predation by baboons on immature baobab fruit, which reduced the fruit available for mature seed production by up to 85%, with major consequences for population stability (Chapter 8). There was high inter-annual variability in fruit production, with a two and a half fold difference between the highest and lowest year, but the cause of this variation could not be identified. Lastly it was found that a high proportion (41%) of adult trees produced less than 5 fruit per year. These trees were termed 'poor-producers' and were equated with the 'male' trees described by local people across Africa. To help in understanding this tendency, the flowering patterns of these trees were described in Chapter 5, with speculation as to possible causes.

2.3 Phenology and fruit-set

Flowering (Chapter 5) followed a steady-state pattern starting in October and November and continuing until April. Leaf flush (Chapter 5) took place in the same months, but responded more quickly to early rain than did flowering. There was no difference in flower number or fruit-set between land-use types. However, trees in villages tended to produce more flowers and flowered for longer than in other land-use types. Flowering and fruit production were highly variable between years, and thought to be influenced by the previous season's conditions. There was a significant difference between years in the number of flowers produced, but no significant difference in fruit-set; likewise, flowering, not fruit-set, increased with tree size and life-stage. Thus it would seem that variation in fruit production between years is a consequence of reduced flower production and not the capacity of trees to set fruit.

The majority of adult trees produced between 200 and 600 flowers; 9% produced >1000 flowers and 4% produced <49 flowers per year. Adult trees that produced from 50-400 flowers had the highest average fruit-set of 30%. After this fruit-set declined with flower numbers, and trees that produced <50 flowers did not produce any fruit. Up to 23% of adult trees did not set fruit at all, and 31% had a fruit set of <1%.

On investigating the difference in flowering patterns of poor-producers versus producer trees, it was found that there was no difference in the number of flowers produced, length of flowering and peak flowering, but that there was a significant difference in fruit-set. Possible causes of low fruit-set were discussed in terms of plant age, environmental variables, inadequate pollination, genetic aberrations and sexual dimorphism.

2.4 Recruitment

Results show that baobab recruitment is micro-site limited rather than seed-limited (Chapter 6). Baobabs produce large quantities of seed, a high proportion (>86%) of which is viable and forms persistent seed banks for at least two years. The exceptions occur in areas inhabited by baboons, where fruit predation results in seed limitation, in turn resulting in poor recruitment (Chapter 8). Seedling emergence in such areas was extremely slow and staggered over two growing seasons.

Poor rainfall is given as the reason for poor seedling survival in many other regions, but it is more likely that mortality is a result of inconsistent intra-seasonal rainfall than low rainfall *per se*. Where plants were protected from livestock, the majority of seedlings survived only three weeks and 94% died before any follow-up rainfall. As many as 35% of saplings in closed plots died of moisture stress either soon after planting or just before the rains. A further limiting effect is the high level of livestock damage, particularly in human-modified landscapes. Here, repeated livestock browsing and trampling was responsible for 86% of sapling mortality. After being browsed for the first time, plants tended to flush more leaves, but after repeated browsing events, many plants died, probably due to depletion of stored reserves.

2.5 Socio-economics

The harvesters tended to be unemployed, middle aged women with little or no schooling (Chapter 7). The majority were involved in the informal sector, working as labourers and vendors, and many also received government child or pension grants. All harvesters used and sold NTFPs, and these contributed, respectively, 33% and 14% to their annual income. It was found that the cash value derived from the sale of baobab fruit for commercial utilization was four times higher than its subsistence value. The annual cash income received from baobab fruit alone made up 38% of the total annual sales of all NTFPs. The subsistence use of the fruit has diminished and it now has a lower subsistence value than other NTFP food items. At the same time, cash earned from the sale of baobab fruit was found to help alleviate poverty, improve livelihoods and allow harvesters to

participate in a cash economy by investing in other businesses and by paying for livelihood needs that require cash, such as food, education and transport.

2.6 Sustainable harvest levels

A population matrix model (Chapter 8) was used to predict baobab population trends in the five land-use types, and these were used to suggest sustainable harvest levels. Parameters used in the model were derived from external studies and from the results in this thesis, namely: fruit production (Chapter 4), phenology (Chapter 5) and recruitment (Chapter 6). The model indicated that, in the absence of fruit predation and under moderate or low livestock numbers, baobabs have a high tolerance to fruit harvesting and can sustain fruit harvest levels of up to 96%. However, fruit predation by baboons in nature reserves and high livestock numbers, particularly in human-modified landscapes, can cause the baobab population to decline if action is not taken to boost recruitment.

3. Management recommendations

This study found that baobabs have a high tolerance to fruit harvesting, but that other factors may have a major negative impact on population stability, resulting in low to zero sustainable harvest levels. High livestock numbers, land transformation, fruit predation, leaf harvesting and infrequent rainfall have a major impact on recruitment, and bark harvesting, elephant bark stripping and disease affect adult tree survival. Management and mitigation of these impacts are crucial to maintain future baobab populations.

Mitigation can be attempted by direct harvesting interventions, additional management practices and landscape-level management (Ticktin, 2004). Harvest-level mitigation entails control over the frequency and quantity of fruit collection, but it is felt that this would be difficult to control in an open- access situation, and, considering the other threats, would have the least impact on sustainability. Additional management practices, which include sowing seeds and the planting of saplings are recommended. Saplings need to be protected until they escape the browse trap, and thus should be planted in areas where they can be easily monitored. At the landscape level, the reduction of livestock numbers would be beneficial, but, considering the importance of livestock to rural communities, this is unlikely to be a practical solution. It is recommended that a culture of protecting young trees should be encouraged by creating awareness of the vulnerability of baobab populations. Baobab population stability is very sensitive to adult tree survival, and thus bark harvesting, which is known to kill trees, and removal of adult trees for other land-use needs must be strongly discouraged.

Domestication and assisted colonization has been suggested as a means to improve baobab productivity, to relieve the pressure on wild populations and protect the species from decline caused by climate change. However, the success of domestication relies on fast growth and high fruit production, which in turn relies on access to abundant water. Due to the scarcity of water in the study area, this would be an impractical mitigation strategy. On the other hand, growing baobabs in high rainfall areas outside these environments would help supply a growing demand for baobab products and protect the species from decline. Extensive work in domestication is currently being undertaken in West Africa (Jensen *et al.*, 2011), which could help guide local initiatives.

Baobabs are iconic trees and stand like majestic statues in the African savanna landscapes. Baobab products have been harvested by human populations for many thousands of years and in modern times baobab fruit maintains a high value by contributing to the alleviation of poverty and the improvement of livelihoods. Thus government agencies, businesses, traditional authorities and harvesters need to invest in mechanisms that will protect baobab trees and ensure their survival for millennia to come.

4. Achievements and uniqueness of this study

This study has considerably advanced our understanding of baobab ecology:

- The assessment of fruit over three years, across different size classes and over five land-use types, represents the most thorough assessment of baobab fruit production yet published.
- Baboons have been known to eat immature fruit, yet this is the first quantitative assessment of the baboon damage.
- Livestock is often blamed for poor baobab recruitment, but this is the first study to quantify its effect on seedling and sapling survival.
- This is the first study to quantify baobab population flowering and fruit-set and to do this over sequential years.
- Valuation techniques have been used for a number of NTFPs, but this is the first time it has been applied specifically to baobabs.
- Despite the importance of baobab fruit, this is the first published study that has attempted to determine sustainable harvest levels.

5. Future research areas

The introduction (Chapter 1) provided a review of what is already known about baobab ecology. This study has contributed substantially to furthering our knowledge in this field; however there is still a lot we do not know. Below is a list of areas that were revealed by this study and that need further attention. It is not an exhaustive list, but represents themes related to this study.

- The ecological effects of harvesting (Chapter 8) need further investigation. Studies should not be limited to fruit harvesting, but should also include the impacts of leaf and bark removal, and how all types of harvesting interact within different land use areas. Questions asked could include: Does the removal of leaves affect caterpillar populations, or result in reduced carbon sequestration? How does the removal of fruit affect fauna and flora, and how do nesting animals react to frequent visits to the trees?
- It is not clear why there is a much lower use of baobab leaves in southern Africa compared to West Africa. Do leaves not taste the same? Is there a wider choice of edible herbs in southern Africa and therefore baobab leaves are not the first choice? Are baobab leaves seen as a drought food and thus have a lower 'social acceptance'?
- Ownership and access rights to trees have not been clearly defined, particularly where collection takes place in open-access areas.
- Baobab diseases are still not well understood. Elsie Cruywagen, a plant pathologist at the University of Pretoria, has been isolating and identifying fungi found on baobab trees, but this research still has a long way to go. Baobab seedlings and fruit have been found to be diseased with unidentified pathogens (personal observation). Similar symptoms have been found on baobab fruit in Malawi (Chimuleke Munthali, personal communication). So far, adult mortality appears to result from a combination of drought stress and disease and occurs episodically, but if fruit and seedlings are also affected, it will be critically important to understand these threats.
- Why do baobabs exhibit staggered germination, and what inhibition factors control this? It is not simply a lack of moisture, as unscarified seed in well-watered nurseries are known to stagger germination over at least three years (Hofmeyr, 2003)(personal observation).
- Why do baobab trees become hollow (cavitation)? Very little is known about the process of ageing. Baobab researcher, Diana Mayne, believes that cavitation is necessary for baobab architecture, allowing support for its huge size as it gets larger. It also, of course, brings about a reduction in mass relative to volume. Baobabs also tend to lose limbs or parts of limbs as they get bigger; is this part of the same process? The large Makulu Makete tree which was dated by Patrut et al. (2010) collapsed when it was

seemingly healthy with no sign of disease. Surprisingly, the tree was not hollow and instead the centre was filled with brown rot. Was this tree in the process of cavitation and could not withstand the sudden weakness caused by the rot?

- Not enough work has been done on the pollination biology of baobab flowers. For years it has simply been accepted that bats are the main pollinators. In West and East Africa bats are known to visit flowers, but it appears that this has never been seen in southern Africa. Von Breitenbach and Von Breitenbach (1974) spent four weeks camping under a baobab tree, observing flowering, but never mentioned bat visitations. During the fieldwork for this study, many nights were spent looking out for bat visitations and bat enthusiasts were invited to place mist nets around trees to catch bats, but fruit-eating bats were never caught. According to local bat experts, fruit-eating bats only move into the area in January when sycamore figs and other trees are in fruit, but few baobabs are still in flower. On the other hand, thousands of hymenoptera (bees and wasps) swarm around baobab flowers after anthesis in the early mornings (Watson, 2007; Wickens and Lowe, 2008) (Colin Bristow personal communication; personal observation). Bat and baobab distributions may overlap, but if bats are not around during peak flowering season (November and December), to what extent do hymenoptera pollinate baobab flowers and how does this affect baobab breeding systems? It is hard to believe that more extensive work has not yet been done on this.
- As pointed out in Chapter 5, the breeding biology of baobabs is still very poorly understood, and in particular the reason for so-called 'male' trees. How prevalent are 'male' trees in the population? How long do they stay fruitless? What reason and mechanism drives this 'behaviour'? Is it due to environmental variables, inadequate pollination, genetic aberrations or a breeding strategy?
- Comparative studies from other parts of the baobab distribution would be extremely useful to understand the extent of observed variation, as from this study we now know so much more about baobab phenology and fruit production at the southern limit of their distribution.
- Conversely, comparative and collaborative work on the focus areas of genetic variation, tree improvement systems, quality of leaf and pulp, management of baobab market gardens, vegetative propagation and climatic adaption to drought in southern Africa would be valuable. A great deal of work is being done in these study fields in West Africa, where a multi-disciplinary team, supported by the European Union and the Danish government (Danida), have focussed on knowledge gaps required to support baobab domestication and preservation of the species (Jensen *et al.*, 2011), as suggested above.

- In South Africa three long-term monitoring plots are in existence, each set up at different times, by unrelated researchers to measure baobab demographic information. The first is referred to as Skelmwater, a 3 hectare area, near the town of Messina, established in 1931 to measure annual girth growth and is the oldest baobab growth data plot in existence. The second established in 1987 is situated in Musina Nature Reserve, and consists of two transects running north-south and east-west, 9.6km x 20m and 12km x 20m respectively. Here permanently marked trees are assessed every ten years for growth, recruitment and mortality. The third plot is situated in an area where commercial fruit harvesting is taking place on communally managed land, in northern Venda. Here 106 permanently marked trees in five land-use types are monitored annually; these measurements were initiated by this PhD study in 2007. Trees are assessed for flower and fruit production, disease and growth. At present these plots are being monitored by volunteers and independent researchers who have a passion and interest in baobab research, but for sustainable long term research, the monitoring of these plots needs to formalized and funded. A research trust could be set up to support long-term monitoring and to co-ordinate other baobab research in the area.

6. Conclusion

The harvesting and commercialization of wild NTFPs present social, economic and environmental challenges (Berkes and Folke, 1998). Thousands of NTFPs are harvested from wild populations around the world and the uses of these products provide for the subsistence and commercial needs of many millions of people (Shackleton *et al.*, 2007). Yet very few of these products are being sustainably harvested, constituting a threat to many ecosystems (Boot and Gullison, 1994; Ticktin, 2004). The management of such resources requires a broad approach, integrating human needs and environmental variables (Belcher *et al.*, 2005). Resource users, forest managers, traders, global business and researchers play important roles in the fate of these natural resources, as do environmental variables (Belcher *et al.*, 2005). Fortunately, there is a growing recognition of the responsibility of all stakeholders in the sustainable management of NTFPs. This is evident in the increasing number of certification programmes such as ‘Fair Trade’ and ‘Organic’. Furthermore, the Convention on Biodiversity led to many countries developing legislation that protected both resources and resource users from exploitation (Crouch *et al.*, 2008). There is also a growing body of scientific literature on the ecological consequences of harvesting NTFPs (Ticktin, 2004). As the commercial interest in NTFPs grows into millions of US dollars,

studies on biological, economic and social aspects will play an ever more valuable role in the sustainable management of our natural resources.

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Appendices

Appendix 1: Participant Information Sheet

Participant Information Sheet

Harvesters

How do I participate in the research?
As a harvester, you are invited to participate in interview. The interview will be conducted in the village where you reside. The interview will be a series of questions and should not take longer than an hour to complete.

Does participation in the interview cost me anything?
Participation in the interview will not cost you anything. If there are any costs, the researcher, Sarah Venter, will ensure that you are fully reimbursed.

If I decide not to participate or to withdraw, will I be penalized in any way?
Participation in this interview is voluntary and refusal to participate will not involve any penalty or loss of benefits to which you are is otherwise entitled. You may also withdraw, at any time, without penalty or loss of benefits.

Do I have to answer all the questions?
No, you do not have to answer all the questions. Only answer the questions that you want to answer. You will not be penalized if you do not answer all the questions.

Is the information I give during the interview confidential?
Your name will not appear on any of the questionnaires. This will ensure that your answers and opinions will remain confidential.

Why is this research proposed?
This research aims to learn more about sustainable harvesting of baobab fruit. The importance of baobab trees will be described and how the utilization of the trees can contribute to local peoples' livelihoods.

How will this benefit me?
A better understanding of the ecology and use of baobabs in northern Venda will help manage the resource sustainably to ensure future benefits.

How long will this research take?
Interviews are being conducted during the months of June and July 2009. The data will be analyzed and written up towards the end of 2009 and beginning of 2010. Final results and presentation of the data will aim to take place in June 2010.

Who can be contacted?
Sarah Venter from the School of Animal, Plant and Environmental Sciences, University of Witwatersrand is doing this research. She lives 100km from the study site in Louis Trichardt and can be contacted at:

Cell: 082 374 9534
Email: windwaai@mweb.co.za
PO Box 203, Louis Trichardt, 0920

Appendix 2: Interview consent and contact details form

Harvesting of baobab products in northern Venda, Limpopo Province

Participant Consent

I have read/ have been read the information on the participant information sheet.
I understand that I am participating in research and not treatment.
I understand that participation in this research is voluntary and that I am free to withdraw from the research at anytime without prejudice.

Participant Signature _____

Interviewers Signature _____

Witness Signature _____

Confidential Contact details Form

Interview details

Interviewers name _____

Questionnaire number No 1 ☐ No 2 ☐ No 3 ☐

Interview number _____

Date of Interview _____

Place (Village name) _____

Time of interview _____

Contact details of interviewee

Interviewees Code _____

Interviewees Name _____

Cell number _____

Address _____

_____

Appendix 3: Socio-economic Questionnaire No.1

Socio-economic Questionnaire No. 1

Detailed Harvester Questionnaire

30 Respondents. Interviews taking place in the village or home.

I Questionnaire Information

Date _____

Names of Interviewers _____

Village _____

Interview no. _____

II Respondent information

1 Code Name _____

2 Age

Under 16 ☐ 16 - 30 ☐ 30 - 50 ☐ 50 + ☐

3 Sex

Female ☐ Male ☐

4 Education

None ☐ Std. 5 ☐ Std. 8 ☐ Matric ☐

Tertiary ☐ University ☐ Other _____

5 Employment

Unemployed ☐ Employed ☐ Informal ☐

6 Occupation

Laborer ☐ Trader ☐ Domestic Worker ☐ Other ☐

7 Personal Income

None ☐ R100 - R500 p/m ☐ R500 - R800 p/m ☐ R800 + p/m ☐

8 Social Grant

None ☐ Pension ☐ Child Grant ☐ Disability Grant ☐

9 Relation to head of household

Head ☐ Wife ☐ Mother ☐ Daughter ☐

Other _____

10 Number of dependents

Children ___ Adults ___ Elderly ___ (write number)

III Household Information

11 Number of people in the household

Youth <16 ___ Women 16 - 50 ___ Men 16 - 50 ___ Elderly 50 + ___

12 Number of people educated in the household

None ___ Std 5 ___ Std 8 ___ Matric ___

Tertiary ___ University ___ Other _____

13 Number of people employed in the household

Unemployed ___ Employed ___ Informal ___

14 No of people receiving social grants in the household

None ___ Pension ___ Child Grant ___ Disability Grant ___

15 Total cash income to the household

None ☐ R100 - R500 p/m ☐ R500 - R800 p/m ☐ R800 + p/m ☐

IV General Non-Timber Forest Product use

16 What products do you collect from the bush for household use?

		Y/N	How important are these products? *	How often do you collect them?**	Do you sell these products? If so how much do you earn?***
	Firewood (list species)				
16.1	Mopani				
16.2					
16.3					
16.4	Other general				
	Insects (list species)				
16.5	Masonga				
16.6	Grasshoppers				
16.7	Stinkbugs				
16.8	Termites				
16.9					
16.10					
	Fruit (list species)				
16.11	Marula Fruit (Mafula)				
16.12	Berchemia (Munee)				
16.13					
16.14					
	Spinach (list species and plant parts)				
16.15					
16.16					
	Medicine (list species and plant parts)				
16.17					
16.18					
16.19					
	Meat (list species and parts)				
16.20					
16.21					
	Building Material (list species and plant parts)				
16.22	Poles (List sp. below)				
16.23					
16.24					
	Other Products				
16.25					
16.26					
16.27					

* Very important, Important, not that important

** Every day in season, Once a week in season, Only when I need it.

*** In season I get R100 - 500pm, R500 - R800 pm, R800+ pm

17 Where do you sell the products?

In the village ☐ Neighboring villages ☐ Town ☐ Traders/outsiders ☐

18 What baobab products do you collect?

		P/C/B*	How important are these products? **	How often do you collect them?***	How Much do you collect?****
	Baobab Bark Products				
18.1	Rope making				
18.2	Weaving				
18.3	Medicine				
18.4	Other				
18.5	How do you harvest baobab bark?				
	Baobab Leaf Products				
18.6	Food				
18.7	Medicince				
18.8	Fodder				
18.9	Other				
18.10	How do you harvest baobab leaves?				
	Baobab Root Products				
18.11	Food				
18.12	Medicine				
18.13	Fodder				
18.14	Other				
18.15	How do you harvest baobab roots?				
	Baobab Fruit Products				
18.16	Food				
18.17	Curios				
18.18	Wholesale to traders				
18.19	Other				
18.20	How do you harvest baobab fruit?				

	Baobab Seedlings				
20.21	Food				
20.22	Medicine				
20.23	Other				
20.24	How do you harvest baobab seedlings?				
	Other Baobab Uses/ Products				
20.25					
20.26					
20.27	How do you harvest these baobab products?				

* Past (P) or Current (C) or Both (B)

** Very important, Important, not that important

*** Every day in season, Once a week in season, Only when I need it.

**** Plastic bag, 25kg bag, 50 kg bag, 80 kg bag

19 Do other people in the village or area collect these products?

Yes ☐ No ☐ Comment _____

If the respondent themselves does not collect these baobab products, but other people in the village do, then complete the next question by replacing 'you' with 'they'.

20 Do you sell these baobab products? (apart from to EcoProducts)

		Y/N	If so how much do you earn?*	Where do you sell these products?**	Observed impacts as a result of harvesting?***
	Baobab Bark Products				
20.1	Rope making				
20.2	Weaving				
20.3	Medicine				
20.4	Other				
	Baobab Leaf Products				
20.5	Food				
20.6	Medicince				
20.7	Fodder				
20.8	Other				
	Baobab Root Products				
20.9	Food				
20.10	Medicine				
20.11	Fodder				
20.12	Other				

	Baobab Fruit Products				
20.13	Food				
20.14	Curios				
20.15	Wholesale to traders				
20.16	Other				
	Baobab Seedlings				
20.17	Food				
20.18	Medicine				
20.19	Other				
	Other Baobab Uses/ Products				
20.20					
20.21					

* In season I get R100 - 500pm, R500 - R800 pm, R800+ pm

**In the village, Neighboring villages, town, traders/outsiders

***Reduced leaf production, reduced fruit production, reduced growth, wilting, sickness, death

V Collecting baobab fruit for selling

If answers to the above questions indicate that baobab products, other than fruit, are collected on a large scale or for commercial gain by the respondent, then repeat relevant questions in the this section (V) for each product.

21 How many households are there in your village?

10 - 30 ☐ 30 - 50 ☐ 50 - 100 ☐ 100 + ☐

22 How many of these households collect baobab fruit to sell?

10 - 30 ☐ 30 - 50 ☐ 50 - 100 ☐ 100 + ☐

23 Where do you collect baobab fruit?

Your home ☐ Village in general ☐ Your field ☐ Fields in general ☐

Bush ☐ Hills ☐ Other _____

24 How long does it take you to collect one bag of fruit?

1 day ☐ 1/2 day ☐ 1-2 hours ☐ < 1 hour ☐

25 When collecting fruit, do you use transport or walk?

walk ☐ scotch cart ☐ taxi ☐ private vehicle ☐

26 **Do you have any costs when collecting fruit?**

Yes ☐ No ☐ Comment _____

27 **Does anybody else in your household collect fruit, how many others?**

Yes ☐ No ☐ How many? _____

28 **Does anybody else (not in your home) help you?**

Yes ☐ No ☐ Who? _____

29 **Who do you sell baobab fruit to?**

Sarah ☐ Tourists ☐ Other _____

30 **How much do you earn in a season from selling baobab fruit to ecoproducts?**

Nothing ☐ R100 - R500 p/m ☐ R500 - R800 p/m ☐ R800 + p/m ☐

31 **What do you use this cash for?**

Food ☐ School fees ☐ School clothes ☐ Children's clothes ☐

Settling debts ☐ Building costs ☐ Other _____

32 **Where do you spend your cash?**

In the village ☐ Neighboring villages ☐ Town ☐

33 **Do you think selling baobab fruit benefits you?**

Yes ☐ No ☐ How? _____

34 **Do you think selling baobab fruit benefits your community?**

Yes ☐ No ☐ How? _____

VI General Information about conservation and management of baobabs

35 How many baobabs do you think are found in your area (around your village)?

None ☐ 0 - 100 ☐ 100 - 500 ☐ 500 - 1000 ☐

1000 + ☐

36 Where do you find them? (F - few/ L - lots)

Villages ___ Fields ___ Bush ___ Hills ___

Other _____

37 How long do you think they live for?

10 years ☐ 10 - 50 years ☐ 50 - 100 years ☐ 100 - 500 years ☐

500 - 1000 yrs ☐ 1000 - 2000 yrs ☐ 2000 - 5000 yrs ☐ 5000 - 10 000 ☐

38 Do all baobab trees produce fruit?

Yes ☐ No ☐

39 If not, why do you think so?

_____

40 Does fruit production differ from year to year?

Yes ☐ No ☐

41 If so, why do you think so?

Rainfall ☐ Temperature ☐

Other _____

42 Do you see many young baobabs (1 - 3 year old)?

Yes ☐ No ☐

43 If not, what do you think affects their survival?

Wild animals ☐ Domestic animals ☐ Insects ☐ People ☐

Other _____

44 If animals, describe which animals?

Donkey ☐ Goats ☐ Cattle ☐

Other _____

45 Was there a time when you saw many young baobabs?

Yes ☐ No ☐

46 If yes, when?

1 - 5 yrs ago ☐ 6 - 10 yrs ago ☐ 10 - 20 yrs ago ☐ 20 - 50 yrs ago ☐

47 If yes, what do you think helped their growth?

Lack of animals ☐ Good rainfall ☐ Other ☐

48 **Do you know of baobab trees that have died?**

Yes ☐ No ☐

49 **If yes, how long ago?**

1 - 5 yrs ago ☐ 6 - 10 yrs ago ☐ 10 - 20 yrs ago ☐ 20 - 50 yrs ago ☐

50 **Where?** _____

51 **Did many trees died at the same time?** Yes ☐ No ☐

52 **If yes:**

2 - 5 trees ☐ 5 - 10 trees ☐ 10 - 20 trees ☐ 20 + ☐

53 **What do you think caused their death?**

Drought ☐ Floods ☐ Disease ☐

Other _____

54 **Do you think collecting leaves is damaging to the tree?**

Yes ☐ No ☐ Comment _____

55 **Do you think collecting bark is damaging to the tree?**

Yes ☐ No ☐ Comment _____

56 **Do you think collecting fruit is damaging to the tree?**

Yes ☐ No ☐ Comment _____

57 **Do you think collecting fruit is negatively affecting regeneration?**

Yes ☐ No ☐ Comment _____

58 **Are you allowed to cut down baobabs?**

Yes ☐ No ☐ Comment _____

59 **Are you allowed to pull out baobab seedlings?**

Yes ☐ No ☐ Comment _____

60 **Are baobabs protected?**

Yes ☐ No ☐ Comment

61 **If "yes" by whom**

Headman ☐ Sivic ☐ Government ☐

Other _____

62 **Are baobab seedlings protected?**

Yes ☐ No ☐ Comment

63 **If "yes" by whom**

Headman ☐ Sivic ☐ Government ☐

Other _____

64 **Is there ownership of baobabs?**

Yes ☐ No ☐ Comment _____

65 **If yes, who owns them?**

Individuals ☐ Headman ☐ Herbalist ☐ Government ☐

Other _____

66 **Have you ever planted a baobab?**

Yes ☐ No ☐ If so where? _____

67 **If you were given a baobab seedling, where would you plant it?**

At home ☐ At school ☐ At the shop ☐ Field ☐

Bush ☐ Other _____

68 **Are baobabs culturally important?**

Yes ☐ No ☐ Comment _____

69 **If yes, in what way?**

_____

70 **Do you know of any Venda beliefs or fables about baobabs?**

Yes ☐ No ☐ Comment _____

71 **If yes - record.**

_____

_____

_____

72 **Is there anything else you would like to mention?**

_____

_____

_____

_____

Thank you for participating!

Appendix 5: Socio-economic Questionnaire No.2

Socio-economic Questionnaire No. 2

General Harvester Questionnaire

100 Respondents. Interviews taking place at supply points in the village.

I Questionnaire Information

Date _____

Names of Interviewers _____

Village _____

Interview no _____

II Respondent information

1 Code Name _____

2 Age

Under 16 ☐ 16 - 30 ☐ 30 - 50 ☐ 50 + ☐

3 Sex

Female ☐ Male ☐

4 Education

None ☐ Std. 5 ☐ Std. 8 ☐ Matric ☐

Tertiary ☐ University ☐ Other _____

5 Employment

Unemployed ☐ Employed ☐ Informal ☐

6 Occupation

Laborer ☐ Trader ☐ Domestic Worker ☐ Other ☐

7 Personal Income

None ☐ R100 - R500 p/m ☐ R500 - R800 p/m ☐ R800 + p/m ☐

8 Social Grant

None ☐ Pension ☐ Child Grant ☐ Disability Grant ☐

10 Number of dependents

Children ___ Adults ___ Elderly ___ (Write number)

11 What do you use your baobab cash for?

Food ☐ School fees ☐ School clothes ☐ Children's clothes ☐

Settling debts ☐ Building costs ☐ Other _____

12 Where do you spend your cash?

In the village ☐ Nabouring villages ☐ Town ☐

13 Do you think selling baobab fruit benefits you?

Yes ☐ No ☐ How? _____

14 Do you think selling baobab fruit benefits your community?

Yes ☐ No ☐ How? _____

14.1 Did you use any baobab products before?

None ☐ Fruit ☐ Bark ☐ Other _____

14.2 Did your parents or grandparents use any baobab products?

Parents ☐ Grandparents ☐ Other ☐ Who _____

None ☐ Fruit ☐ Bark ☐ Other _____

14.3 Where baobab trees important in the past?

No ☐ Yes ☐

Uses ☐ Spiritually ☐ Culturally ☐ Other _____

14.4 Are baobab trees still important?

No ☐ Yes ☐

Uses ☐ Spiritually ☐ Culturally ☐ Other _____

15 Is there anything else you would like to mention?

_____

_____

_____

_____

_____

_____

_____

_____

_____

Thank you for participating!